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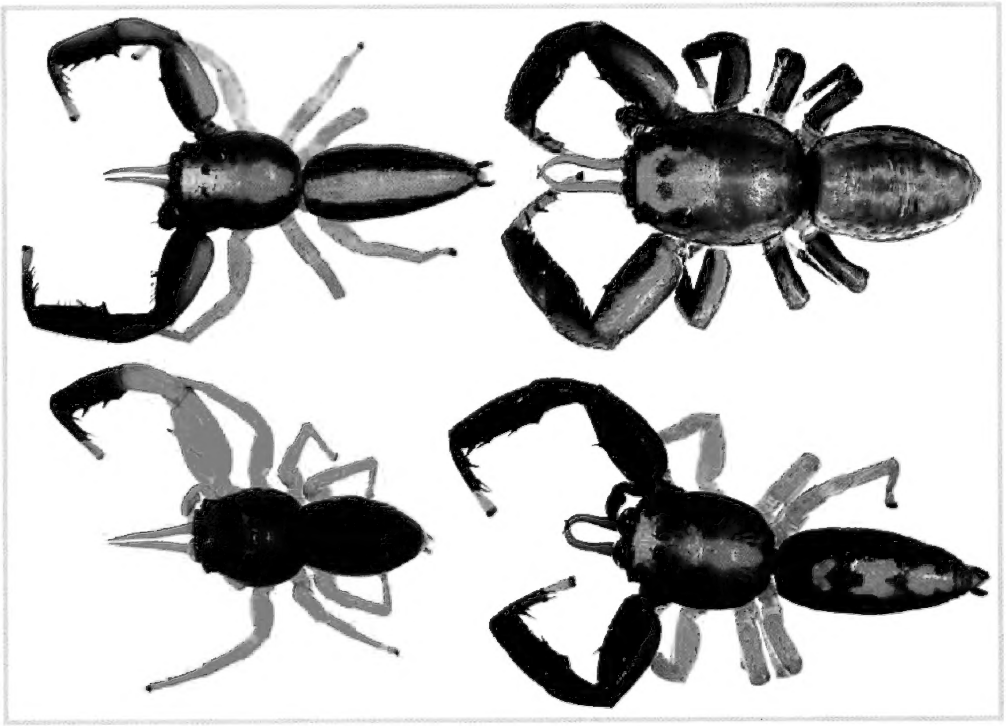

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COVER IMAGE

Diversity among Madagascan spiders of the genus *Padilla*
See Andriamalala, this issue, pp. 243–330.

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Revision of the Genus *Padilla* Peckham and Peckham, 1894 (Araneae: Salticidae) — Convergent Evolution of Secondary Sexual Characters Due to Sexual Selection and Rates of Molecular Evolution in Jumping Spiders

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The horned jumping spider genus *Padilla* Peckham and Peckham is restricted to Madagascar. The genus comprises 15 species, which are herein diagnosed, described, and illustrated in detail. Three synapomorphies of the genus are found. A key to males is provided. Twelve species are new: *P. mazavaloha, P. maingoka, P. manjelatra, P. lavatandroka, P. mitohy, P. griswoldi, P. astina, P. ombimanga, P. mihaingo, P. foty, P. boritandroka,* and *P. ngeroka*. *Padilla javana* is excluded from the genus and considered *incertae sedis* within Salticidae. *Padilla mantis*, *P. glauca*, and *P. lancearea* (Simon 1900) are considered *nomina dubia*. A phylogenetic analysis of 38 morphological characters and two sequenced genes (COI and 28S) exhibit a conflict between the morphological and molecular hypotheses due to convergent evolution of the secondary sex traits such as horn shape. The diversification of cheliceral horns observed in male *Padilla* appears to be sexual selection. The monophyly of the genus has been confirmed both by the Ballinae morphology phylogeny (Benjamin 2004) and the Salticidae 28S phylogeny (Hedin and Maddison 2003). Within Ballinae, *Padilla* is a sister group of the genus *Philates*. Within Salticidae, *Padilla* is a sister group of two balline genera, *Pachyballus* and *Ballus*, with which it forms a monophyletic group that is a sister group to a clade including Marpissoids, Heliophanines, Freyines, Euophryines, and Plexipoids. For the first time, penalized likelihood was used to assess the average rates of molecular evolution of the 28S gene and the ages of the genus and members of the family Salticidae. The ages of *Padilla* (13.06 Mya) and the subfamily Ballinae (23.17 Mya) are too recent for Gondwanan vicariance hypothesis; thus, the stepping stone hypothesis is a better explanation for the distribution.

KEYWORDS: Madagascar, Phylogeny, Horn and life style, convergent evolution, sexual selection, divergence time, Ballinae, Salticidae

The jumping spider family (Salticidae) is represented by more than 5,000 species (Platnick 2006) of varied body forms, behaviors, and ecological relationships. Their unique high-resolution eyes (Land 1985) permit visually mediated predatory behavior (Jackson and Pollard 1996) and complex courtship marked by visual communication, with striking morphological ornamentations (Griswold 1987; Maddison 1988). These secondary sexual characters are proven to be particularly important in jumping spiders, e.g., in the genus *Habronattus*, in which sexual selection for species recognition has played a role in the evolution of male secondary sex traits that are exposed to females during courtship and are known to be associated with prezygotic reproductive isolation and speciation (Griswold 1987; Masta and Maddison 2002).

This study focuses on the genus *Padilla*, an endemic of Madagascar. *Padilla* are small to medium-sized spiders, 4–6 mm in length. Their carapace, which can be low or high, may reflect different life styles documented in jumping spiders by Crane (1949). She recognized "runners" (jumping spiders with low carapace that mostly run and jump only during prey capture) and "hoppers" (refers to jumping spiders with high carapace that mostly jump rather than run). At first sight, *Padilla* resemble pseudoscorpions due to the first pair of legs, which are darker and enlarged compared to the other legs, which are typically pale and slender. The males of this genus display one of the most striking secondary sexual characters: a forward projecting pair of horns on the chelicerae. These horns look like a lance which can be bent near the tip. They have a varying degree of elongation, orientation, and origin in different species.

The genus was described by Peckham and Peckham (1885) based on *Padilla cornuta*. This species was described from a single male specimen from Madagascar and was diagnosed by the presence of straight, stout, and long horns (twice as long as the paturon) originating from the bases of each paturon. After the discovery of six other species, Simon (1900) included *Padilla* within his Bavieae group based on the following characters: (1) depressed cephalothorax, (2) anterior eye row wider than posterior, posterior median eyes closer to anterior laterals, and (3) cephalic region shorter than thoracic. The genus was separated from all other genera within the Bavieae group by (1) a palp short and wider instead of thin and longer, and (2) first legs exaggeratedly thickened. Subsequent tentative placement of the genus has been made by Maddison (1988, 1995) and Benjamin (2004). Both placed the genus within the subfamily Ballinae within the so-called Salticoida group on the basis of two other characters of the male palpi: (1) a well-coiled embolus lying flat on the tegulum, and (2) a tegulum which is divided by a pale, longitudinal furrow. *Padilla*, however, was not represented in their final hypotheses.

Currently, very little is known about the relationship of *Padilla* to other balline genera and nothing is known about the intrageneric relationships. Of seven previously known species, all but one is recorded from Madagascar, *Padilla javana* Simon, 1900, which is recorded from Java. However, the original description is not detailed enough to clarify its position and, unfortunately, the type specimen appears to be lost. This species lacks the extraordinary embellishments present in all male *Padilla* (Prószyński, 2003). Most species *Padilla* are known only from their type specimens, of which only three were located. The aim of this study is to revise the genus, including redescriptions of known species as well as descriptions of new species. A key to species is given and their distributions in Madagascar, correlated with environmental factors, are discussed. The phylogenetic relationships of *Padilla* are examined, and its place within the Salticidae and the Ballinae is assessed for the first time. I have used morphological and molecular data, the latter from two different genic regions (COI, 28S), to generate parsimony and maximum likelihood phylograms.

The nature of these different markers is of value in understanding the behavior of morphological data, such as secondary sexual characters and other somatic characters, contrasted with data from different genic regions in reconstructing phylogeny of *Padilla*. This is the first time that the rates of evolution of the 28S gene in jumping spiders have been documented. Knowledge of the nucleotide sequence rate of evolution inferred from a maximum likelihood tree allowed me to estimate divergence times for this genus and some members of the Salticidae family. I will discuss the biogeographical implications of those results on isolation of *Padilla* in Madagascar.

The presence of horn-like projections on the carapace has already been noted in other spiders (Wanless 1996; Huber et al. 2005). In *Padilla*, the presence of the horns is male biased. They may be used in courtship or male-male combat. The role of sexual selection by female choice in shaping male secondary sex traits has already been documented among insects and other arthropods (Eberhard 1985, 1991; Clark and Uetz 1993; Clark and Morjan 2001; Huber et al. 2005). The diver-

sification of horn, carapace height and body shape observed in *Padilla* may be the result of sexual selection, natural selection, or both. In this paper, I used geospatial and environmental data integrated in ArcGIS 9 and DIVAGIS version 5.2 software as well as a statistical test of correlation among morphological characters and some bioclimatic variables to discuss these alternatives.

Materials and Methods

Conventions.— All anatomical abbreviations are listed in Appendix 2. On the phylograms, nodes that are assigned a letter (e.g., A, B, C, D, B', C') represent a particular group of species or clade. Throughout the discussions of the phylogenetic analysis and relationships among taxa, these letters are used to refer to clades belonging to that node (e.g., clade C, comprising the *Brevis* group, *P. mihaingo, P. mitohy, P. foty,* and *P. maingoka*).

Collections.— Most materials for this study were drawn from a geographically comprehensive collection generated over the last five years from more than 60 sites in Madagascar by the California Academy of Sciences Madagascar Arthropod Survey. Materials from the Muséum National d'Histoire Naturelle in Paris, Royal Museum for Central Africa in Tervuren, and Museum of Comparative Zoology at Harvard University were also examined. In order to assess the diversity of arthropods in Madagascar, the Survey was conducted in sites of varied vegetation, climate, elevation, and geological substrate. Different methods of capture such as Winkler or litter sifting, beating low vegetation, general collecting and pitfall, Malaise traps, light, and yellow pan traps were applied (Fisher 2005). Specimens were preserved in 75% ethanol at room temperature to keep them flexible for morphological work (Martin 1978) and shipped to and deposited in the collections of the Department of Entomology of the California Academy of Sciences.

Description.— I used morphological characters, molecular distances and distributional data to discriminate species. A male and female, if both are known, are described for each species. Species description and illustrations were based on 10 representatives of each species, if possible. Representatives were chosen according to the degree of character variation and site locality to maximize the range of variation and geographic distribution considered. All measurements (Fig. 1) are in millimeters and were taken using an Olympus SZH10 dissecting microscope. The measurements were taken from five males and five females of each species, when possible, and are reported as ranges for each sex. The mean value is also calculated for both sexes. In many species, there were fewer than five individuals of each sex available, or one sex was unknown, so only those numbers are reported (Table 1). Known species are only described to document new information. Examinations of specimens and drawings were made using an Olympus SZH

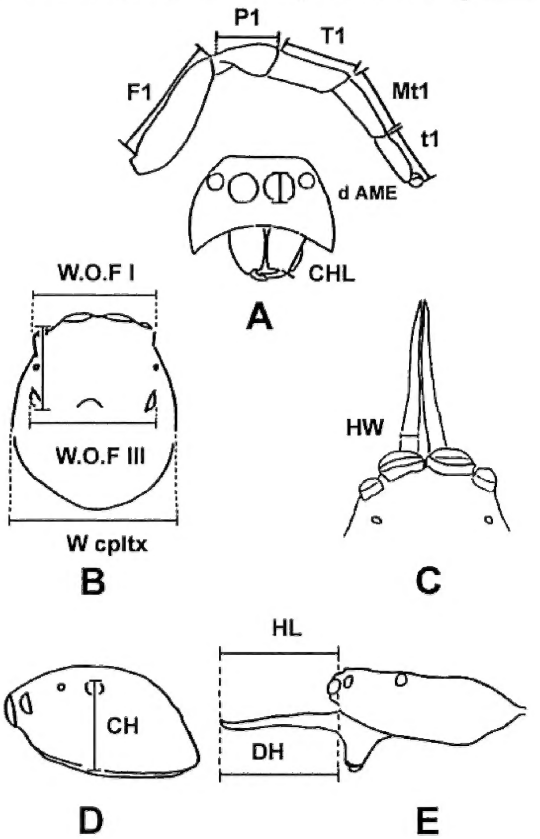

Figure 1. *Padilla* measurements.

TABLE 1. Ratio of the measurements of body, prosoma and legs of *Padilla*.

SPECIES	Number of specimens (♂,♀)	Total L (♂,♀)		Horn L / CL (♂)	CH/ CL (♂,♀)		WOF I/ W cpltx (♂,♀)		W chelic/ CHL (♂,♀)		F1 / WOF II (♂,♀)		F3/ WOF II (♂,♀)		F3/ F4 (♂,♀)		Tb1 / WOF II (♂,♀)	
P. sartor	(1, 0)	5.76	_	0.5	0.31	_	0.70	_	0.80	_	1.36	_	0.82	_	1.12	_	1.20	_
P. mazavaloha	(3, 15)	5.39	0.32	0.41	0.32	0.32	0.76	1.13	0.76	0.94	1.13	1.08	0.69	0.7	1.17	0.83	0.95	0.76
P. maingoka	(2, 0)	6.04		0.38	0.24		0.74		0.80		1.49	_	0.66	_	1.29	_	1.23	_
P. cornuta	(3, 5)	5.14	5.15	0.46	0.31	0.32	0.80	0.90	0.75	0.83	1.28	0.99	0.71	0.6	1.17	0.77	0.96	0.68
P. manjelatra	(2, 1)	5.88	5.76	0.75	0.39	0.4	0.81	0.88	0.64	0.77	1.38	0.97	0.68	0.71	1.38	0.84	1.00	0.70
P. lavatandroka	(13, 10)	5.88	6.67	0.78	0.41	0.38	0.79	0.79	0.62	0.72	1.35	1.16	0.88	0.86	1.11	0.85	0.93	0.83
P. armata	(1, 1)	5.88	5.64	1.63	0.30	0.33	0.70	0.74	0.60	0.73	1.44	0.89	0.85	0.74	1.10	0.86	1.07	0.79
P. griswoldi	(2, 0)	5.4	_	0.53	0.19	_	0.41	_	0.73	_	2.14	_	1.14	_	1.34	_	1.79	_
P. astina	(1, 0)	4.7	_	0.67	0.34	_	0.71	_	0.65	_	1.38	_	0.76	_	1.16	_	1.12	_
P. ombimanga	(1, 0)	5.92	_	0.61	0.30	_	0.69	_	0.70	_	1.38	_	0.75	_	1.21	_	1.21	_
P. boritandroka	(7, 0)	4.55	_	0.04	0.34	_	0.80	_	0.51	_	1.32	_	0.65	_	1.22	_	1.17	_
P. ngeroka	(12, 11)	4.60	4.43	0.22	0.26	0.27	0.81	0.73	0.55	0.88	1.38	0.79	0.62	0.56	1.46	0.73	1.11	0.56
P. mitohy	(0, 9)	_	5.59	_	_	0.27	_	0.82	_	0.87	_	1.09	_	0.69	_	0.76	_	0.82
P. mihaingo	(0, 1)	_	5.53	_	_	0.32	_	0.78	_	0.8	_	1.74	_	1.23	_	0.84	_	1.51
P. foty	(0, 1)	_	4.96	_	_	0.27	_	0.81	_	0.74	_	1.13	_	0.73	_	0.84	_	0.88

Stereo dissecting Microscope equipped with a camera lucida. Photographs of the diagnostic characters were taken using a Nikon DXM1200 digital camera attached to a Leica MZ16 stereomicroscope montaged with the Synchroscopy® Auto montage system pro version 5.01.0005 and were used to generate the final digital images. Female epygina were digested with either KOH under a heat lamp for 3–8 hours, or a proteinase (trypsin or "ReNu": Enzymatic contact lens cleaner, Bausch & Lomb Inc.) overnight. Specimens were soaked overnight in 100% EtOH (transferred from 70% ethanol to absolute ethanol), cleaned with an ultrasonicator, critical point dried with CO_2, sputter coated with AuPd, and scanned with a Leo 1450VP Scanning Electron Microscope (SEM). Automontage and SEM images were saved as TIF files that were edited using Adobe Photoshop. Plates were assembled and labeled using Adobe Photoshop©.

Species distributions were mapped using ArcGIS 9, climatic and ecological conditions were assessed using ArcGIS 9 and DIVAGIS — Worldclim version 3.0.

SPECIES GROUPS.— The new and previously-described species of *Padilla* were divided into four groups based primarily on phenetic similarity in carapace shape (implying a "runner" or "hopper" lifestyle) and male cheliceral horn configuration. For convenience in characterizing and describing species and discussing character distributions, these groups are referred to throughout. I make no *a priori* assumption that these groups represent evolutionary lineages, but test the group monophyly using phylogenetic analysis with morphological and molecular characters, which are discussed below.

armata group
- *P. armata* Peckham and Peckham, 1894
- *P. astina*, new species
- *P. griswoldi*, new species
- *P. ombimanga*, new species

brevis group
- *P. boritandroka*, new species
- *P. ngeroka*, new species

cornuta group
P. cornuta (Peckham and Peckham, 1885)
P. lavatandroka, new species
P. manjelatra, new species
sartor group
P. maingoka, new species
P. mazavaloha, new species
P. sartor Simon, 1900
Unassigned
P. foty, new species
P. mihaingo, new species
P. mitohy, new species

Phylogenetic Analysis

This analysis comprises: (1) a family analysis, (2) a subfamily analysis, and (3) a generic level analysis. First, to test Benjamin's (2004) hypothesis that *Padilla* is a member of Ballinae, I included two species of the genus and one balline genus (*Ballus)* within Hedin and Maddison's (2003) 28S Salticidae tree, which already has one balline genus (*Pachyballus)*, to see if *Padilla* species come out as their sister taxa. Once, the placement of *Padilla* as a Ballinae was confirmed by this analysis, I decided to also add two species of the genus within Benjamin's (2004) Ballinae morphological matrix, since *Padilla* was not included in his sub-family analysis. The intention was (1) to define the placement of *Padilla* within this sub-family, (2) to find its relatives, and (3) to determine the appropriate outgroup taxon. Therefore, characters of the genus were coded according to Benjamin's (2004) matrix and two other characters that are synapomorphies for the genus were added (Appendix 4). These new characters are the path of the sperm duct intermediate between S and C (character 6–1, Fig. 2C) and the presence of cheliceral horns (character 42–1). A subfamily analysis was then performed for 42 characters of 18 balline genera including two species of *Padilla*. Once the outgroup was determined by this analysis, generic analyses were performed both for morphology (Appendix 3) and molecular characters in order to assess species relationships within *Padilla*. Finally, a family level analysis was conducted to (1) determine the exact placement of the genus within the family of Salticidae and to (2) assess the probable placement of the sub-family of Ballinae within the Salticidae. My sequences of the 28S gene of all species of *Padilla* were then analyzed along with all the 28S sequences of 84 other salticid genera, including two other balline genera: *Ballus* and *Pachyballus*, which were contributed by Hedin and Maddison (2003).

Outgroup choice.—The subfamily analysis placed the genus *Philates* as the closest relative of *Padilla*. However, within the phylogeny of Ballinae the species of *Padilla* were nested within the genus *Philates*. This raises the possibility that *Padilla* may be merged with the genus *Philates*. Therefore, the genus *Philates* along with the genus *Ballus* were used as outgroups in the morphological analysis as a test of this hypothesis. *Ballus* was used to root the molecular tree. Even if it is quite distantly related to *Padilla*, its inclusion in this analysis was necessary due to a lack of fresh material of *Philates* for molecular work.

Morphology

Taxa and characters scored.—The characters used in phylogeny inference are assumed to be homologous (Griswold 2001; Hennig 1966) and are evolving independently of each other (Freeman and Herron 2004). Shared derived characters or synapomorphies are preferred over other characters (Hennig 1966). Special consideration was placed on secondary sexual characters such as the

horns and first leg spination. Those characters are conspicuous and highly differentiated, especially in males. In jumping spiders, those secondary sexual characters are often displayed during courtship (Clark and Morjan 2001; Owens 2003) and may function as species isolating mechanisms (Griswold 1987; Masta 2002). The same attention was accorded to complex and functionally important organs such as the male palp and the female epigynum.

Here I describe the character states scored for each of the taxa included in the morphological phylogenetic analyses and give a matrix as a summary (Appendix 3).

Horns

1. *Presence in males:* (0) absent; (1) present (synapomorphy of all *Padilla).*
2. *Horn curvature:* (0) straight and slightly convergent (*cornuta* group *and brevis* groups; Figs. 3A–G, 4A, 5–8); (1) outward and then inward (*sartor* group; Figs. 9A–C); (2) inward, then outward and finally crossed at tips (*armata* group; Figs. 10A–D).
3. *Horn orientation lateral view:* (0) downward curve (*brevis* group; Figs. 3G–H, 11A–B); (1) almost straight or slightly curved downwards toward the tips (*armata* group; Figs. 3E–F, 12A–B, D); (2) present as double curve, first going down, then going up near tips, but tips not surpassing the clypeus (*cornuta* group; Figs. 3A–B, 13A–D); (3) going upward with tips reaching middle of AME (*sartor* group; Figs. 3C–D, 14A, 15A–C).
4. *Horns tips, dorsal view:* (0) not crossed, separated from each other (*cornuta* group, *brevis* group, *sartor* group (in part, only *P. sartor)*; Figs. 8, 9A, 16, 17); (1) crossing each other (*armata* group, *sartor* group (in part, *P. mazavaloha, P. maingoka*); Figs. 9B–C, 10, 18–23).
5. *Horn thickness (horn width/cheliceral width):* (0) slender, mean width<0.15mm (*P. maingoka, P. boritandroka, P. ngeroka*); (1) intermediate, mean width 0.15–0.25mm (*P. sartor, P. cornuta, armata* group); (2) thick, mean width>0.25mm (*P. mazavaloha, P. manjelatra, P. lavatandroka*).
6. *Horn length (horn length/carapace length):* (0) horn L/CL< 0.3 (*brevis* group, *P. maingoka*); (1) horn L/CL: 0.3–0.6 (*sartor* group except *P. maingoka, P. cornuta, armata* group); (2) horn L/CL> 0.75 (*P. manjelatra, P. lavatandroaka*).
7. *Horn origin:* (0) from the distal part of the chelicerae near the fangs or CHL/DH<= 0.25 (*brevis* group; Figs. 3G–H); (1) from the proximal part of the chelicerae or CHL/DH>0.5 (all other *Padilla*; Figs. 3B, 3D–F, 12–13, 15).

Leg spination

8. *Femur I midventral spine and bristles:* (0) absent (outgroup taxa); (1) one or two midventral spines and two retromarginal bristles present (all *Padilla*, Figs. 24A–D).
9. *Femur I proximoventral spines:* (0) only one (all *Padilla* except *P. sartor* and *P. ombimanga*); (1) two (*P. sartor, P. ombimanga*; Figs. 16, 21, 25A).

Femur II and III dorsal

10. *Additional promarginal spine:* (0) absent (*P. mihaingo* and *P. mitohy, P. mazavaloha, Ballus*); (1) present (all *sartor* group except *P. mazavaloha, all armata* group, all *cornuta group*, all *brevis* group; Fig. 25D).

Femur IV dorsal

11. *Male patella I spur:* (0) absent (all *Padilla* except *P. manjelatra, P. lavatandroka*); (1) present, proventral (synapomorphic to *P. manjelatra, P. lavatandroka*; Fig. 25B).
12. *Femur and patella I retromarginal setal fringe:* (0) absent (outgroup); (1) present (all *Padilla*).
13. *Tibia I width:* (0) as wide as other leg segments (all other *Padilla*; Figs. 24A–C); (1) clearly broader or wider than femur, patella and metatarsi (*P. boritandroka, P. maingoka; P. mihaingo, P. mitohy, P. ngeroka*; Figs. 24B–C).
14. *Tibial spur:* (0) absent (all *Padilla* except *P. mazavaloha* and *cornuta* group); (1) present (*P. mazavaloha* and *cornuta* group; Fig. 25C).

15. *Tibia I proximoventral distal spine:* (0) larger than the proximals (all *armata* group and *P. sartor*; Fig. 24A); (1) of the same size or smaller than the proximals (Fig. 24D).
16. *Tibia and metatarsus I coloration:* (0) same as other segments; (1) clearly darker than other leg I segments (*P. manjelatra* and *P. lavatandroka*; Fig. 24D).
17. *Tibia and metatarsus I spines:* (0) paired, present both on proventral and retroventral sides of the tibia and metatarsus (all *Padilla* except *P. armata*, *P. astina*, and *P. griswoldi*); (1) not paired, only proventral spines present (all *armata* group except *P. ombimanga* (Fig. 25A).

Carapace

18. *Fovea presence:* (0) absent (*P. foty, P. ngeroka*); (1) present.
19. *Carapace edge:* (0) carapace with lateral whitish bands of scales (*P. astina, P. griswoldi, P. mihaingo; P. mitohy;* Fig. 27A–B); (1) carapace without lateral whitish bands of scales.
20. *Implied Life style (carapace height/carapace length):* (0) "runner" or CH/CL lesser than 0.25 (*brevis* group, *P. maingoka, P. mihaingo, P. foty*; Figs. 28C–D); (1) "intermediate" or CH/CL: 0.30–0.35 (*armata* group, *P. cornuta, P. sartor, P. mazavaloha*; Fig. 28B); (2) "hopper" or CH/CL greater than 0.35 (*P. manjelatra, P. lavatandroka;* Fig. 28A).
21. *Cephalothorax shape:* (0) almost rectangular (*brevis* group, *P. maingoka, P. mitohy, P. mihaingo*; Figs. 17, 23, 27,29A–B); (1) "trapezoidal" interiorly narrowed and enlarged between leg II and III (all other *Padilla* and *Philates*; Figs. 4A–C); (2) nearly square, or cephalothorax width = CL (*Ballus*).

Mouth parts

22. *Clypeus border:* (0) clypeus edge with a fringe of white scales (*P. mihaingo, P. mitohy*, all *Armata* group except *P. ombimanga*; Fig. 14C); (1) clypeus edge without a fringe of white scales (Figs. 14A–B, D–E).
23. *Endite shape:* (0) elongate and parallel sided; (1) enlarged and epically expanded (*Armata group, P. manjelatra, P. lavatandroka;* Fig. 30B).
24. *Endite ridge:* (0) located only along the anterior part of the endites as a serrula (*P. foty*); (1) extending past the serrula, reaching to the lateral bases of endites (all other *Padilla*; Fig. 30D).

Chelicerae

25. *Chelicerae edges:* (0) Sharpened or carinate on both lateral margins (*brevis* group; Figs. 14D–E); (1) normal, not having a sharp longitudinal edge along lateral sides or carinate only on upper outer distal margins (all other *Padilla).*
26. *Cheliceral dorsum:* (0) flattened dorsally (synapomorphy of the *Brevis group*, Figs. 14D–E); (1) not dorsally flattened.
27. *Cheliceral width:* (0) wider or chelicerae width/chelicerae length>0.60 (*P. lavatandroka, P. manjelatra*; Fig. 14B); (1) thinner, chelicerae width/chelicerae length<0.60 (*brevis group*; Figs. 14D–E).
28. *Paturon orientation compared to carapace:* (0) paturons not projected forward but rather at 90° from carapace (Fig. 3B); (1) paturons projected forward much more than 90° from the carapace (*brevis* group; Figs. 3H–11B).

Sternum

29. *Sternum anterior part:* (0) oval, anterior part slightly truncated; (1) almost round, anterior part not truncated (*P. lavatandroka, P. manjelatra*; Fig. 30A); (2) almost round, but anterior part truncated (*P. sartor* and *P. ombimanga*).

Abdomen

30. *Abdomen dorsal:* (0) flattened (*P. astina, P. griswoldi*; Fig. 12B–C); (1) not flattened (Figs. 13B–C, 15A).
31. *Spinneret plate:* (0) spinnerets preceded by large half circle ventral plate; (1) without this plate.

Palp

32. *Embolus fold* (*ef*): (0) present (*brevis* group, *P. mazavaloha*; Figs. 31D–E, 32B–D–E); (1) absent.
33. *Embolus coil tilt*: (0) inclined to the retrolateral side (*brevis* group, *P. mazavaloha*; Figs. 31D, 32A–D); (1) not (all other *Padilla*).
34. *Embolar second loop* (*esl*): (0) thickened (*brevis* group, *P. mazavaloha;* Figs. 31D–E, 32D); (1) not thickened (Fig. 29A–D–G).
35. *Tegular groove* (*tg*): (0) absent (*brevis* group and *sartor* group, *Ballus*. sp; Figs. 31A–D–G, 32E–D); (1) shallow (*cornuta* group except *P. cornuta*; Figs. 29E–H); (2) deep (*armata* group and *P. cornuta*; Figs. 29B, 33B–D–H).
36. *Ventral tegulum posterior knob* (*vk*): (0) absent (all other *Padilla*); (1) present (*armata* group; Figs. 33B–E–G).

Epigynum

37. *Interconnection of copulatory opening (co):* (0) interconnected (*P. mihaingo, P. mazavaloha, P. manjelatra*; Fig. 27D); (1) not interconnected (*P. mitohy, P. foty*; *P. cornuta*; *P. ngeroka;* Figs. 26A–B–E–F, 27C–E).
38. *Sulci (sclerotized tube following copulatory openings):* (0) absent (most *Padilla)*; (1) present (*P. foty, P. mitohy*; Figs. 26A–B–E–F, 34E–G).

Cladistic Analysis of Morphological Data

PAUP version 4.0b.10 (Swofford, 2001–2002) was used to perform both the subfamily and the intrageneric phylogenetic analysis. I conducted a heuristic search with a random stepwise addition of 1000 replicates subjected to tree bisection-reconnection (TBR) branch swapping. All characters were unordered and equally weighted. Analyses using successive character weighting (Farris 1969; Carpenter 1998), using the maximum value of the rescaled consistency index was also performed to obtain trees that maximize implied weight across all characters. Only the most parsimonious trees were retained. I used MacClade 3.0 and 4.0 (W.P. Maddison and D.R. Maddison 1992, 2000) to optimize characters on the tree. If optimizations were ambiguous, they are resolved using the ACCTRAN option (Accelerated transformation; Farris optimization), which favors secondary loss over convergence to explain homoplasy and therefore maximizes homology (Hormiga 1994; Griswold et al. 1998; Schuh 2000). Uninformative characters were excluded before the calculation of tree statistics. Character state changes were traced with MacClade version 4.0 (W.P. Maddison and D.R. Maddison 2000).

Molecular Analysis

Genus molecular analysis.— To determine the relationships within the genus *Padilla*, a total of 15 taxa, of which 14 species are from the genus *Padilla*, were included in the analysis (Table 2). Two individuals were sequenced for each species for *P. lavatandroka*, *P. mazavaloha*, *P. cornuta*, *P. manjelatra*, *P. ngeroka*, for a total of 19 individuals from 14 species in the genus *Padilla*. The genus *Ballus* was used as the outgroup taxon to polarize the character states of the ingroup and to establish the position of the root.

Note: *P. armata* was not included in the molecular analysis because of a lack of good DNA material. This species is only known from very old type specimens.

Family level molecular analysis.— The placement of the genus inside the family Salticidae was assessed by combining and analyzing the 28S sequences of the genus with the 28S sequences of 84 other salticid taxa from the molecular phylogeny of Hedin and Maddison (2003).

DNA isolation.— Field collected specimens were placed in 75% EtOH and kept in the museum collection until the time of DNA extraction. Total genomic DNA was isolated by grinding two entire legs in lysis buffer (Buffer ATL and Proteinase K) with a Teflon grinding implement. The

TABLE 2. List of all specimens sequenced for molecular phylogenetic analysis: DNA, collection localities, gene bank accession numbers, museum accession numbers.

Species	Localities	COI	28S	Museum accession No.
Ballus chalybeius	SE Azerbaijan, Lenkoran	EF514383	EF514398	CASENT9021988
***Sartor* group**				
Padilla sartor	Antsiranana, Montagne d'Ambre	EF514373	EF514388	CASENT9021839
Padilla mazavaloha	Fianarantsoa, PN Ranomafana	EF514374	EF514389	CASENT9006891
Padilla maingoka	Fianarantsoa, PN Ranomafana, Talatakely	EF514370	EF514386	CASENT9003506
***Cornuta* group**				
Padilla cornuta	Antananarivo, Andranomay	EF514381	EF514396	CASENT9004193
Padilla lavatandroka	Antsiranana, Montagne d'Ambre	EF514375	EF514390	CASENT9021901
Padilla manjelatra	Antsiranana, R.S Manongarivo	EF514382	EF514397	CASENT9021862
***Armata* group**				
Padilla griswoldi	Fianarantsoa	EF514380	EF514395	CASENT9021858
Padilla astina	Toliara, Ifaty	EF514378	EF514394	CASENT9021860
Padilla ombimanga	Antsiranana, Montagne d'Ambre	EF514372	EF514387	CASENT9023432
***Brevis* group**				
Padilla boritandroka	Mahajanga, PN Tsingy de Bemaraha	EF514371	EF514385	CASENT9009733
Padilla ngeroka	Antananarivo, Andranomay	EF514376	EF514391	CASENT9004188
Unassigned				
Padilla foty	Antsiranana, RNI de Lokobe	EF514369	EF514384	CASENT9021859
Padilla mitohy	Antsiranana, Andavakoera	EF514377	EF514392	CASENT9011933
Padilla mihaingo	Antsiranana, Ampondrabe	EF514379	EF514393	CASENT9011958

homogenate was incubated at 55°C until tissue dissolved (may take up to 48 hours or more) and then purified using DNeasy™ Tissue Kit (Quiagen Inc., Valencia, CA) following the manufacturer's protocols.

POLYMERASE CHAIN REACTION (PCR) AMPLIFICATION.— For each specimen, a fragment of approximately 500 base pairs in length of mitochondrial gene COI and 800bp in length of nuclear gene 28S was amplified via PCR. Double stranded DNA was amplified, with some volume modifications depending on the specimen, in the following reaction: 25µL volume reaction of 12.88–13.88µL PCR water, 2.5µL of 10X PCR buffer (as supplied by the manufacturer of Taq polymerase) or 5µL of Expand High Fidelity ^{Plus} PCR buffer (as supplied by the manufacturer of Expand High Fidelity ^{Plus} Taq), 2.5µL MgCl2 (10mM), 2.5µL dNTP (10mM), and 1.25µL of each primer, 0.12µL Amplitaq® DNAPolymerase (Applied Biosystems Inc., Foster City, CA) or Expand High Fidelity ^{Plus} Taq (Roche). PCR amplification primers for these fragments are listed in Table 3. All reactions were initially denatured at 94–95°C for 2–5 minutes in a MJ Dyad Thermal Cycler (MJ Reasearch, Waltham, MA) or a DNA Engine Dyad, Peltier Thermal cycler, then subjected to 35 cycles of 30s denaturation at 94–95°C, 30s annealing at 49°C for 28S, 45°C for COI, and 45s extension at 72°C per cycle, with a final 10 min extension at 72°C. Amplified products were cleaned using the UltraClean PCR clean-up Kit (MoBio, Solana Beach, CA) prior to sequencing.

SEQUENCING.— All sequencing was done using dye terminator cycle sequencing following the protocol specified by ABI PRISM™ Dye terminator Cycle Sequencing Ready Reaction Kit (Revision B, August 1995, Perkin-Elmer, Norwalk, CT). Primers used for amplification served as sequencing primers. Additional internal primers were designed for sequencing purposes (Table 3)

TABLE 3. Primer sequences for amplification and sequencing of mitochondrial COI,Nuclear large subunit (28S) rDNA divergent domains D1-D3. Reference listed in Hedin and Maddison 2001a and Simon 1994.

Primer	Sequence	Utility	D. mel REF	Primer citation
C1 - N - 2776	5' -GGA TAA TCA GAA TAT CGT CGA GG- 3'	amplification / sequencing	25351 - 6	Simon et al. (1994)
C1 - J - 2309	5' -TTT ATG CTA TAG TTG GAA TTG G- 3'	amplification / sequencing	25351 - 9	Simon et al. (1994)
28S - C	5' -GGT TCG ATT AGT CTT TCG CC- 3'	amplification / sequencing	25351 - 12	Hedin and Maddison (2001)
28S - 0	5' -GAA ACT GCT CAA AGG TAA ACG G- 3'	amplification / sequencing	25351 - 16	Hedin and Maddison (2001)
28Sint - F	5' -CGG AGC CAT CCT RCG ATT C- 3'	amplification / sequencing	22352403	This study
28Sint - R	5' -GAG TGG GCG GAA TCG YAG- 3'	amplification / sequencing	22352404	This study

to provide overlapping sequence coverage for the entire region of 28S. All samples were sequenced in both the forward and reverse directions by way of an ABI 3100 DNA sequencer using a capillary machine.

SEQUENCE ALIGNMENTS.— Mitochondrial and nuclear gene sequences were analyzed and initially aligned using the computer programs Sequencing Analysis 3.4 (ABI Prism™ 1999) and Sequencher 3.1.1 (GeneCodes 1998), respectively. The conserved regions were identified and aligned, and gaps were assigned to minimize changes using ClustalX 1.9a169 (Thompson et al. 1997). The aligned data set was then further manually aligned using MacClade 4.03 (D.R. Maddison and W.P. Maddison 2001) and PAUP*4.0b10 (Swofford 2001). The same process was performed for the combined 28S aligned sequences of salticid genera (Hedin and Maddison 2003) and *Padilla* 28S sequences.

PRELIMINARY SEQUENCE ANALYSIS.— Base composition bias was calculated (Irwin et al. 1991) for the entire fragment. A value of zero indicates no bias and a value of one indicates complete bias. A chi square test in PAUP*4.0b10 (Swofford 2001) was used to test for heterogeneity of nucleotide frequencies among taxa.

PHYLOGENETIC ANALYSIS OF MOLECULAR DATA.— Phylogenetic analysis is reconstructed from the sequence data by using parsimony and maximum likelihood. All analyses were performed using PAUP*4.0b10 (Swofford 2001). Data from different genic regions (COI, 28S) were analyzed first separately as different genes are expected to have different evolutionary dynamics. The two data partitions were combined after their phylogenetic congruence was assessed using the incongruence length difference (ILD) test (Farris et al. 1994) implemented in PAUP*. A single analysis combining data from all genes has the advantage of being based on more data than any single analysis and evolutionary history is best assessed by using datasets from distinct sources (Wheeler et al. 1993). Confidences on clade credibility are both based on results from separate and combined analysis.

Parsimony: Search was performed using the random stepwise addition option of the heuristic search for 1,000 replicates with tree bisection-reconnection (TBR) branch swapping, collapse of zero-length branches, and equal weighting of all COI and 28S characters. All ambiguously aligned sites were excluded. Only the mostly parsimonious trees were retained and summarized with a strict consensus tree.

Maximum likelihood: To determine which model best fit, the dataset was subjected to Modeltest 3.06 (Posada and Crandall 1998) and the resulting Akaika information criterion was used. Once the best-fit model of evolution was found, a heuristic search was executed using the initial parameter estimates obtained from a neighbor-joining (NJ) tree generated in PAUP*. The parameters of the better tree found were re-estimated and the search was repeated. This process was continued until a tree converged on the same maximum likelihood tree. For both parsimony and maximum likelihood, I characterized the reliability of each phylogenetic hypothesis by resampling the original dataset 1000 times using the non–parametric bootstrap (Felsenstein 1985; Hillis and Bull 1993).

The maximum likelihood model was also used to determine whether (1) *Padilla* combined 28S and COI sequences and (2) all the 28S Salticidae sequences are evolving at a constant rate and fit a molecular clock (Felsenstein 1993). I used a procedure proposed by Felsenstein (1993) to test for a molecular clock. This test uses a likelihood ratio test (LRT) to determine if there are significant differences between the likelihood scores obtained from an analysis where the branch lengths are unconstrained as compared to an analysis where the branch lengths are constrained so terminal ends are contemporaneous. The likelihood test statistic was assumed to be approximately equal to an χ^2 distribution with n-2 degrees of freedom, where n equals the number of taxa sampled (Felsenstein 1981).

ESTIMATION OF DIVERGENCE TIMES AND RATES OF MOLECULAR EVOLUTION FOR SALTICIDAE.— The LRT test statistic for the 28S Salticidae data was significant ($2\Delta L = 2[-22284.10856 - (-22636.34008)] = 704.464$, $P<0.001$ ($df = 96$)), meaning that there is rate inconstancy across lineages. In absence of a molecular clock, it is appropriate to use the penalized likelihood (PL) method implemented in the program r8s version 1. 7.0 for estimating divergence times. This method allows rates of evolution to vary substantially across lineages to accommodate branch-length differences in the input likelihood tree; however, it attaches a "penalty" cost to limit rate variations on neighboring branches (Sanderson 2002). The smoothing parameter (λ) governs the degree to which differing rates on neighboring branches are to be penalized. A cross validation criterion was used to select the optimal level of smoothing that best fit the data. A 30 million year old fossil specimen of the genus *Lyssomanes* was used as a minimum age calibration point (Miguel and Penny 2003). The minimum age of 30 million years was then assigned to the node representing the hypothetical common ancestor between *Lyssomanes* and the large clade that includes the Salticoida division. During initial cross validation runs, it was observed that the results were unstable unless a fixed age constraint was placed on the age of the root. Optimization routines in penalized likelihood generally need at least one fixed node (Sanderson 2006 in r8s version 1.7 User's Manual). Based on the analysis of Penney et al. (2003), who assembled data from 830 spider fossils, fossils of the family Salticidae and their relatives were recorded only during the Cenozoic and were all less than 65 million years old (figure 2 in Penney et al. 2003). Thus, fixing the root at 65 million years gives a conservative estimate.

CHARACTER MAPPING.— The "horn curvature" and the "life style" reflected by the carapace height were mapped onto the resulting genus maximum likelihood tree. The carapace height is described as a ratio of the cephalothorax height (CH) divided by the length of the carapace (CL) (Fig. 1). The horn curvature character is divided into the character states: (0) "horn straight and slightly convergent" (Fig. 3A); (1) "horn presenting a simple curve, going outward and then inward" (Fig. 3C); (2) "horn presenting a double curve", going inward, then outward, and finally crossed at tips (Fig. 3E). Crane (1949) defined the "runner" and "hopper" lifestyles in jumping spiders. She suggested a correlation between these lifestyles and carapace height based on the presence of the extensor muscles responsible for the jumping power within the carapace. Those with a high carapace she called "hoppers": these have strong muscles in their carapace that allow them to jump more often. Conversely, those with a low carapace and weaker muscles, these Crane called "runners", run most of their time and jump only during prey capture. For the sake of a hypothesis, here I infer these salticid life styles in *Padilla*, even though nobody has yet made detailed observations on *Padilla* biology. Therefore, if the mean CH/CL of a species is greater than 0.35 and the carapace is greatly enlarged between leg II and III, the "life style" state is assumed to be "hoppers". If the mean CH/CL of a species is between 0.30–0.35 and the carapace is just trapezoidal, the "life style" is assumed to be "intermediate" between "hoppers" and "runners". If the mean CH/CL is less than 0.25 and the carapace is almost rectangular, the "life style" state is assumed to be "runners".

In species of *Padilla* and across the family of Salticidae, I have noticed four kinds of body shape: (1) elongate (*P. cornuta, P foty*; *P. sartor; P. mazavaloha;* Figs. 8A, 9A–B, 34C); (2) beetle like (*Armata* group, Fig. 10); (3) scorpion like (*brevis* group; *P. mihaingo*; *P. maingoka; P. mitohy;* Figs. 9C, 17, 34A–B); (4) high or protruding (*P. manjelatra, P. lavatandroka*; Fig. 8B–C). This character was not included in the phylogenetic analysis because it could not be considered as a phylogenetically independent character. However, in order to investigate whether these four kinds of body shapes are related to species phylogeny or species environmental conditions, I decided also to map them on the resulting molecular tree and correlate them with environmental factors.

Results

Morphological Analyses

Placement of Padilla within Subfamily Ballinae.— The first parsimony analysis of 42 unordered and equally weighted characters of 18 balline taxa, including two species of *Padilla*, produced 26 most parsimonious trees of 85 steps, consistency index of 0.56 (CI), and retention index of 0.64 (RI). Repeated analysis with successive weighting (Farris 1969; Carpenter 1988), using the maximum value of the rescaled consistency index, resulted in three most parsimonious trees. The consensus of these trees (Fig. 35) has a length of 40 steps, a consistency index (CI) of 0.77, and a retention index (RI) of 0.83. This tree is presented as the preferred hypothesis of generic interrelationships within the Ballinae. Within this tree *Padilla* form a well supported monophyletic group (99% bootstrap support) with two synapomorphic characters: path of the sperm duct intermediate between S and C (**6-1**) and cheliceral horns present (**42-1**). The two species of *Padilla* were placed as sister group to *Philates chelifer* based on one synapomorphy: size of translucent septum (sv) small (**19-1**).

Phylogenetic relationships within genus *Padilla*.— The first analysis of 38 equally weighted characters under parsimony produced three most parsimonious trees, with a length of 76 steps, consistency index of 0.61 (CI), and retention index of 0.72 (RI). The analysis was repeated after successive character weighting (Farris 1969; Carpenter 1988), using the maximum value of the rescaled consistency index. This analysis produced three trees (length = 34 steps, CI = 0.82, RI = 0.89), identical in topology to the three most parsimonious trees produced in the unweighted analysis. The consensus of these three trees is considered as the preferred hypothesis of *Padilla* species relationships (Fig. 36).

The monophyly of the genus *Padilla* is resolved at Node D, well supported (97% bootstrap) by three synapomorphies: (1) presence of horns on male chelicera (**1-1**), F1 with one or two midventral spines and two retromarginal bristles (**8-1**), F1 and Pt1 with a retromarginal fringe of setae (**12-1**). The cladistic analysis splits the genus into three major clades A, B, and C.

Clade A: supported by 66% bootstrap includes all *armata* group and *P. sartor*. Within this clade, the monophyly of the *armata* group is well supported (93% bootstrap) by three synapomorphies: horn presenting a double curve on dorsal view (**2-2**), laterally almost straight with tips curving downwards (**3-1**), and palp with a ventral tegulum posterior knob (**36-1**). The group including *P. armata*, *P. griswoldi* and *P. astina* is strongly supported (89%) by two more synapomorphies: Tb1 and Mt1 with unpaired spines (**17-1**), and clypeus border with a fringe of white scales (**22-0**). Likewise, sister grouping between *P. griswoldi* and *P. astina* (87% bootstrap) is supported by two more synapomorphies: carapace edge with lateral whitish bands of scales (**19-0**), and abdomen dorsally flattened (**30-0**).

Clade B: includes *P. mazavaloha* and the *cornuta* group. Within this clade, sister grouping between *P. manjelatra* and *P. lavatandroka* is strongly supported (100% bootstrap) by five synapo-

morphies: horn length implied by the ratio HL/CL>0.75 (**6-2**), presence of male Pt1 proventral spur (**11-1**), Tb1 and Mt1 coloration darker than other leg segment (**16-1**), sternum almost rounded with anterior part not truncated (**29-1**), and palp tegular groove shallow (**35-1**). The monophyly of the *cornuta* group is weakly supported (58% bootstrap) by one synapomorphy: horn laterally presenting a double curve (**3-2**). The placement of *P. mazavaloha* as a sister taxon of the *cornuta* group was weakly supported (61% bootstrap) by the morphological synapomorphy: presence of tibial spur on the first legs (**14-1**).

Clade C: supported by 70% bootstrap, includes the *brevis* group, *P. maingoka*, *P. mitohy*, *P. mihaingo* and *P. foty*. Within this clade, the monophyly of the *brevis* group is strongly supported (100% bootstrap) by four synapomorphies: horn laterally going downward (**3-0**), horn originating from the distal part of the chelicerae near the fangs or CHL/DH<= 0.25 (**7-0**), and thinner reflected by the ratio CW/CHL<0.60 (**27-1**); paturon projected forward (**28-1**). Sister grouping between *P. mihaingo* and *P. mitohy* is also strongly supported (95% bootstrap) by three synapomorphies: absence of an additional promarginal spine on F3 and F4 (**10-0**), carapace with lateral whitish bands of scales (**19-0**), and clypeus border with a fringe of white scales (**22-0**).

NOTE.— The placement of *P. maingoka* within this major clade is unclear. It constitutes the only difference among the three most parsimonious trees which placed it either (1) with the *brevis* group, (2) with the group including *P. mihaingo* and *P. mitohy* or (3) as the sister taxon of the group including these four species. This group of species excluding *P. foty* is supported (87% bootstrap) by three synapomorphies: horn slender, implied by the ratio horn width/cheliceral width<0.15mm (**5-0**), horn length implied by the ratio horn L/CL< 0.3 (**6-0**), Tb1 clearly broader or wider than femur, patella and metatarsi (**13-1**). All members of clade C are united by one more synapomorphic character: cephalothorax almost rectangular (**21-0**).

The cladistic analysis splits all *Padilla* species into three major clades (A, B, C) and confirms the monophyly of all the groupings hypothesized on horn morphology except for the sartor group, whose members are scattered within the three major clades.

Molecular Analysis

Phylogenetic relationships within genus *Padilla*

This study produced a final aligned 1137 base pair (bp) fragment for each taxon, consisting of 759 aligned bp for 28S and 378 aligned bp for COI. The aligned fragment contained 222 sites (115 sites for COI, 107 sites for 28S) that were variable (19.52%) and 129 sites (81 sites for COI, 48 sites for 28S) that were parsimoniously informative (11.34%). Examination of base composition in the entire data set resulted in the following: A: 0.1986; C: 0.2335; G: 0.30054; T: 0.2673. The entire combined data set exhibited 0. 09 base composition bias for all characters and 0.1702 for only variable characters; a Chi-square test for homogeneity of base frequency among taxa was 4.435390 (df = 42) when all characters were included and 30.784074 (df = 42) when constants were excluded, resulting in P values of 1 and 0.899559, respectively. The heterogeneity test suggests that the sequences have roughly the same base composition (are not heterogeneous). The COI data set revealed a base composition bias for only variable characters (0.41). This is mainly due to variation within third positions. However, inspection of the entire COI (0.26) and combined data set (0.09) did not reveal any extreme bias. So this heterogeneity bias does not appear to present a problem for phylogenetic interpretation.

Phylogenetic analysis of COI DNA

The parsimony search found 5 trees of 215 steps, CI = 0.61, RI = 0.58 (Fig. 37A). The maxi-

mum likelihood analysis of the COI data partition using GTR+G+I model of sequence evolution results in one tree with a –ln L= 1614.30907 (Fig. 38A).

Phylogenetic analysis of 28S DNA.— The parsimony search found 2 trees of 165 steps, CI = 0.77, RI = 0.71 (Fig. 37B). The maximum likelihood analysis of the 28S data partition using GTR+G+I model of sequence evolution results in six trees with a –ln L= 1879.24764 (Fig. 38B).

Phylogenetic analyses of combined 28S and COI DNA.— The parsimony analysis of all characters resulted in one tree of 436 steps, CI = 0.64, RI = 0.58 (Fig. 39). The best fit maximum likelihood model for both 28S and COI separately and combined, determined using the Akaika criteria in Modeltest 3.06 (Posada and Crandall 1998) was the General Time Reversible with gamma rates variation and proportion of invariable sites (GTR+G+I). The maximum likelihood search in PAUP using this model resulted in one maximum likelihood tree with a –ln L= 3771.21431 (Fig. 40). Maximum likelihood was also used to test for molecular clock. The likelihood ratio test (LRT) statistic is $2\Delta L = 2[- 3771.21431 - (- 3775.54665)] = 8.6646$, $P = 0.7978 > 0.001$ (df = 13). The molecular clock assumption was not rejected for the combined *Padilla* data set, which indicates that the rate of neutral evolution accumulated in the different sequences was constant over time across the species of *Padilla*. Therefore, branch length for maximum likelihood tree of *Padilla* can be interpreted as divergence times.

Relationships within *Padilla*.— The placement of all taxa did not conflict in the trees obtained from the COI and 28S data, except for the placement of *P. cornuta* which was the sister taxon of *P. ngeroka* in the COI hypothesis (Figs. 37A–38A), whereas it was at the base of the clade including *P. astina* and *P. griswoldi* in the 28S (Fig. 37B). The ILD test for congruence among data partition found a P value greater than 0.01 suggesting that combining the data will improve or at least will not reduce phylogenetic accuracy despite the differences between the COI and the 28S hypotheses (Cunningham 1997).

The combined parsimony and maximum likelihood analysis of 28S and COI data each resulted in one tree. The maximum likelihood analysis (Fig. 40) split *Padilla* species into three major clades A, B', C'. Both parsimony and maximum likelihood analyses agree on clade C'; but members of clades A and B', although grouped in the same order do not form a clade in the parsimony analysis (Fig. 39).

Placement within the Salticidae

The monophyly of the genus *Padilla* within the Salticidae was strongly supported by the parsimony (94% bootstrap) and maximum likelihood tree produced from 832 bp of 28S sequences of 98 salticid taxa (Hedin and Maddison 2003) to which I added 14 species of *Padilla* and one balline genus, *Ballus* (Figs. 41–42). *Padilla* was placed as a sister group of two other balline genera, *Ballus* and *Pachyballus*, with which it forms a monophyletic group that is sister group to the clade including marpissoids, heliophanines, freyines, euophryines, and plexipoids.

Estimation of divergence times and rates of molecular evolution

The cross validation analysis selected $\lambda = 10^{7.5}$ as the optimal value of the smoothing parameters that best fit the data. The divergence time analysis was carried out in the absence of rate constancy across lineages or molecular clock, the average rates of molecular evolution of the 28S genes estimated from the penalized likelihood method is $1.064 \pm 0.104 \times 10^{-8}$ substitutions per sites per years (S/S/Y). A summary of the average rate variation across taxa and the estimated ages of some taxa are given in Table 4.

TABLE 4. Estimated ages and substitution rates of the 28S gene in jumping spiders.

Reconstruction method: Penalized likelihood
Smoothing factor = 31622777
Penalty function = Ancestor-Descendant
Optimization via Truncated-Newton (TN) method with bound constraints
Fossil: Lyssomanes assigned a minimum age of 30Ma
Root fixed-age constraint: 65Ma
Rates are for branches subtending indicated node
Rates are in units of substitutions per site per unit time

Node	Estimated age) (Ma)	Estimated rates (x10-8)/ sites/ year
Unident _ spartaeine - Portia	38.73	1.0219
Salticoida	31.67	1.1571
Ballinae	23.17	1.1750
Padilla	13.06	1.1594
Heliophanines	13.05	1.1378
Freyines	9.77	1.0619
Euophryines	5.74	1.0844
Marpissoids	3.99	1.0183
Plexippoids	3.76	1.0902
Plexippines	2.93	1.0959
Pellenines	1.89	1.0675

Summary of rate variation (substitutions per site per year)

Mean = 1.064×10^{-8}
Std Dev = 0.104×10^{-8}
Min = 0.803×10^{-8}
Max = 1.295×10^{-8}
Range = 0.492×10^{-8} Ratio = 1.613

DISCUSSION

This is the first taxonomic treatment of this genus since Peckham and Peckham (1894) and Simon (1900). This study has recognized 15 species of *Padilla*, twelve of which are newly described; however, many more species are expected to be discovered. This is also the first morphological and molecular study to examine phylogenetic relationships among members of the genus *Padilla*, and the first time the relationships of this genus to members of the subfamily Ballinae and family Salticidae have been phylogenetically analyzed.

Molecular data contrasted with morphology data

Even if the species composition within clades A, B' and C' (Fig. 40) of the maximum likelihood analysis is almost the same as species composition within clades A, B, C (Fig. 36) in the morphology parsimony analysis, the arrangement of taxa inside these major clades is slightly different, e.g.,

Clade A: in the molecular analysis, sister grouping of *P. sartor* and *P. ombimanga* are strongly supported both by parsimony (100% bootstrap) (Fig. 39) and maximum likelihood (100% bootstrap) (Fig. 40). Those taxa share six morphological apomorphies but did not form a clade in the morphology hypothesis (Fig. 36).

Clade B': the *cornuta* group and the *brevis* group each break apart. *P. cornuta* (*cornuta* group) and *P. ngeroka* (*brevis* group) form a strongly supported sister group pair (96% bootstrap support

for parsimony, Fig. 39; 96% for MLE, Fig. 40): these were not associated in the morphology analysis (Fig. 36).

Clade C': *P. foty* and *P. mitohy* are strongly supported sister taxa (74% bootstrap both for parsimony and MLE). *P mihaingo* is well supported as their sister taxon (100% bootstrap both for parsimony and MLE). *P. boritandroka* (*brevis* group) remained within the same clade and form a well supported clade with these latter (88% bootstrap for both parsimony and MLE).

All the groups based on horn morphology, body shape and implied "life style" were paraphyletic in the molecular hypotheses, except for the sister group relationship between *P. griswoldi* and *P. astina* which remained strongly supported by both parsimony and MLE (100% bootstrap), as did the relationship between *P. manjelatra* and *P. lavatandroka* (100% bootstrap).

Character mapping

When the discrete characters describing, 'horn curvature' and "implied life style" are mapped onto the maximum likelihood tree, it is shown that the double curved horn of the *armata* group (Fig. 3E), simple curved horn of the *sartor* group (Fig. 3C) and straight horn of the *cornuta* and *brevis* groups (Figs. 3A–G) have evolved more than once (Fig. 43). Likewise, implied lifestyle showed homoplasy. Only two "hoppers", *P. manjelatra* and *P. lavatandroka,* formed a natural group (Fig. 44).

The results of the phylogenetic analysis revealed a conflict between the morphological and molecular hypotheses suggesting convergent evolution of the cheliceral horns, carapace height and body shapes, which are the most conspicuous characters differentiating species of *Padilla*. Yet, leg spination has proven to be more efficient in uniting natural groups such as *P. ombimanga* plus *P. sartor*, *P. griswoldi* plus *P. astina,* as well as all members of clade C' (all with enlarged Tb1).

Origin of the diversification of morphological characters

In *Padilla*, secondary sexual characters, somatic characters and the four types of body shape have evolved convergently when mapped into the molecular phylogeny. These different morphological forms may represent an adaptation to local environmental conditions or forms that may promote reproductive success. Variations in these traits could either be the results of natural selection, sexual selection or both. In order to investigate which of these alternatives might be probable in *Padilla*, I use environmental information and environmental niche modeling taken from distribution data of *Padilla* (Worldclim-DIVAGIS version 5.2) (Table 5). These data allowed estimation of some environmental parameters such as the annual temperature and precipitation, mean temperature of the wettest and driest quarter, precipitation of the wettest and driest quarter, altitude, vegetation and ecological niche quality of the localities where each species occurs and correlated these parameters with morphological data. If horn morphology and body shape correlated with specific ecological conditions of the locality, the diversification of those characters seen in *Padilla* could possibly be the result of natural selection. If these characters were uncorrelated with specific ecological conditions of the locality, their evolution may be due to sexual selection.

Sympatric sister species occurring under similar ecological parameters

I noticed two unusual cases of sympatric sister species with different horn morphology, carapace height and body shape collected from localities that have similar ecological conditions: *P. ngeroka* (*brevis* group, "runner") and *P. cornuta* (*cornuta* group, "intermediate") are sister species according to the molecular analyses (Figs. 39, 40). Their distributions overlapped in two sites: in

TABLE 5. Species, characters and bioclimatic variables from DIVAGIS (Worldclim)

Species	Body shape	Horn	Annual mean T° (°C)	Annual P° (mm)	Mean T° of wettest quarter (°C)	Mean T° of driest quarter (°C)	P° of wettest quarter (mm)	P° of driest quarter (mm)
P. sartor	Elongate	Sartor group	20.1917	1367	21.6333	18.9000	815	66
P. mazavaloha	Elongate	Sartor group	21.1833	1351	22.5333	19.9167	821	62
P. mazavaloha	Elongate	Sartor group	18.5250	1610	21.2333	16.8333	862	123
P. mazavaloha	Elongate	Sartor group	24.2667	1829	25.4167	22.2167	1142	48
P. mazavaloha	Elongate	Sartor group	20.0833	1355	21.5500	18.7667	809	65
P. maingoka	Scorpion like	Sartor group	18.5250	1610	21.2333	16.8333	862	123
P. cornuta	Elongate	Cornuta group	17.5792	1323	20.1000	14.1500	800	56
P. cornuta	Elongate	Cornuta group	18.5250	1610	21.2333	16.8333	862	123
P. cornuta	Elongate	Cornuta group	17.4125	1406	19.5000	14.1833	900	18
P. cornuta	Elongate	Cornuta group	17.5792	1323	20.1000	14.1500	800	56
P. cornuta	Elongate	Cornuta group	17.4125	1406	19.5000	14.1833	900	18
P. cornuta	Elongate	Cornuta group	19.7916	1452	22.1667	17.3333	918	195
P. manjelatra	Protruding	Cornuta group	22.7792	1677	24.0500	20.6833	1053	38
P. manjelatra	Protruding	Cornuta group	15.9417	1558	18.2667	13.9167	799	142
P. manjelatra	Protruding	Cornuta group	22.2833	1416	23.7833	20.1667	791	95
P. lavatandroka	Protruding	Cornuta group	20.1917	1367	21.6333	18.9000	815	66
P. lavatandroka	Protruding	Cornuta group	21.1833	1351	22.5333	19.9167	821	62
P. astina	Beetle like	Armata group	23.2667	367	25.6500	20.7667	498	98
P. griswoldi	Beetle like	Armata group	18.9375	1770	21.5167	17.2167	936	139
P. griswoldi	Beetle like	Armata group	16.6625	1310	21.2333	16.8333	862	123
P. ombimanga	Beetle like	Armata group	21.1833	1351	22.5333	19.9167	821	62
P. boritandroka	Scorpion like	Brevis group	24.2667	1829	25.4167	22.2167	1142	48
P. boritandroka	Scorpion like	Brevis group	23.4708	1318	24.7333	22.2667	841	53
P. boritandroka	Scorpion like	Brevis group	23.7625	1437	25.1333	21.7333	808	97
P. boritandroka	Scorpion like	Brevis group	26.3208	1030	28.2167	23.1333	727	7
P. boritandroka	Scorpion like	Brevis group	22.7792	1677	24.0500	20.6833	1053	38
P. boritandroka	Scorpion like	Brevis group	26.4125	1250	27.4333	24.2833	951	7
P. ngeroka	Scorpion like	Brevis group	17.5792	1323	20.1000	14.1500	800	56
P. ngeroka	Scorpion like	Brevis group	17.8375	1503	20.5333	16.1333	802	117
P. ngeroka	Scorpion like	Brevis group	17.6833	1461	21.2333	16.8333	862	123
P. foty	Elongate	Unassigned	25.4000	2024	26.6000	23.5000	1213	86
P. mitohy	Scorpion like	Unassigned	23.8583	1553	24.9500	22.0000	966	56
P. mitohy	Scorpion like	Unassigned	24.3292	1488	25.4500	22.5000	937	58
P. mihaingo	Scorpion like	Unassigned	25.6500	1384	26.9500	24.4167	756	113

the evergreen rain forest of Ranomafana (Central Southeastern region) and in the broadleaf deciduous forest of Andranomay (Central region) (Figs. 45, 46). The average ecological conditions of the points where *P. ngeroka* was collected were not much different from *P. cornuta*'s: mean annual temperature: 17.7°C and 18.05°C respectively; mean annual precipitation: 1431 mm and 1420 mm, respectively; altitude: (900–1410m) and (1000–1300m). Similarly, the molecular analyses (Fig. 39, 40) suggested sister group relationships between another sympatric pair: *P. sartor* (*sartor* group) and *P. ombimanga* (*armata* group). Not much of a difference in ecological conditions was noticed for these sympatric sister species except for the occurrence of *P. sartor* at the forest edge (Fig. 47, 48) (Table 5). There are additional cases of species of disparate morphology occurring together under conditions of similar ecology. Many species exhibiting different horn morphology, carapace height and body shape were found to occur next to each other at 1300 m in the evergreen mountain rainforest of Montagne d'Ambre (Northern region), i.e., *P. sartor* (*sartor* group), *P. ngeroka* (*brevis* group), *P. lavatandroka* (*cornuta* group) and *P. ombimanga* (*armata* group) and at 900m elevation at the same locality in Ranomafana (Central Southeastern region), i.e., *P. cornuta* (*cornuta* group) and *P. maingoka* (*sartor* group).

Species with similar horn shape, carapace height, and body shape were found to occur in very different environmental conditions

The most striking is the case of the *armata* group: *P. griswoldi* and *P. astina* are sister species in all analyses (Fig. 36, 39–40) and share seven morphological features including horn type, carapace height and body shape. Yet, *P. griswoldi* was found in the Eastern central rain forest of Ranomafana at elevation of 1150–1300 m, 17.8°C mean annual temperature and 1540 mm mean annual precipitation, whereas, *P. astina* occurs in a dry spiny forest of the South, at elevation of 20 m , 24.4°C mean annual temperature, 367 mm mean annual precipitation.

From these observations and a simple statistical test of correlation between horn curvature, body shape and some bioclimatic variables provided by Worldclim version 3.0 (annual temperature and precipitation, mean temperature of the wettest and driest quarter, precipitation of the wettest and driest quarter; Figs. 49–50), horn morphology and body shape appeared to be uncorrelated with ecological conditions such as temperature, precipitation, vegetation type, altitude and niche quality in *Padilla*. Even if there are few cases where species of similar morphology have been found around the same locality, they were not sympatric and therefore their ecological conditions might differ slightly. Consequently, the diversification of the cheliceral horn observed in *Padilla* could be driven by sexual selection. Thus, with respect to the male-biased presence of the horns, I find their presence only on males compelling evidence for sexual selection. Knowing male and female jumping spiders to coexist in the same habitat and therefore, under the same ecological pressure (predators, competitors) and roughly performing the same activity (Alroth 2005); the presence of the horns only among males appears to be in favor of the sexual selection hypothesis and cannot be explained by any other hypothesis such as predation or character displacement. These horns are conspicuous and tactile and might be used both in male fights for mates (contest) or in female choice (Anderson 1994). Moreover, a case of diversification of cheliceral projections due to female choice has already been observed in pholcid spiders (Huber et al. 2005). Therefore, the most probable explanation for the high rate of diversification of cheliceral horns among *Padilla* species is sexual selection.

However, with regard to the body shape and implied lifestyle, no firm conclusion should be drawn before further study of behavior and ecology and more field work is completed. Even if different body shapes and implied life styles were not related to any environmental conditions that have been investigated (Fig. 50), those characters are observed in both males and females. In addition, the estimation of these environmental factors might be too coarse compared to the size of these spiders to be able to detect fine-scale microhabitat variations that could affect their morphologies (i.e., environmental data estimated from 90 m above ground might be inadequate to depict microhabitat differences that could be important to arthropods). Moreover, inasmuch as carapace height and/or "implied life style" appear to be related to modes of locomotion (Crane 1949), data on the nature of substrate might be needed.

Evolution of the horns and body shape

The generic molecular clock combined with the phylogenetic hypotheses allow me to infer the evolution of some conspicuous morphological characters through time in *Padilla*. *Padilla* appears to have evolved 13.06 million years ago from an ancestor that did not have a horn and was beetle like. The general tendency observed from the phylogram (Figs. 40, 43) suggests that *Padilla* horns were primitively double curved (basal part of clade A, members of the *armata* group), evolved through a simple curve to become straight and long in the *cornuta* group, remained straight but shortened in part of the *brevis* group, and then evolved to become a simple curve again. Finally, more derived species of *Padilla* have straight and very short horns (*P. boritandroka*). Concerning

body shape and implied life style, *Padilla* appears to have begun as beetle-like spiders with an intermediate life style, evolved into "*hoppers*" and then "runners", with some species reverting to an intermediate lifestyle; however, all more recent species of *Padilla* are "runners" (Figs. 40, 44).

Rates of substitutions and estimated ages of the genus and some members of the Salticidae

This is the first time the rates of substitution of the 28S gene have been reported for jumping spiders. My results seem to be comparable with those of Brower's (1994) estimation of the rate of evolution of mitochondrial DNA (COI) in arthropods (2.3% sequence divergence per million years or $2.3 \times \lambda 10^{-8}$ substitutions per sites per year), because nuclear DNA is known to evolve more slowly than mitochondrial DNA (Caccone et al. 2004). Mean rates based on the penalized likelihood method for the 28S gene in salticids and their relatives was $1.064(\pm 0.104) \times 10^{-8}$ substitutions per sites per year. Note that Brower (1994) used pairwise divergences to calculate their rate, whereas I used penalized likelihood.

Most salticids are recently diverged. The oldest estimated divergence date is 38.73 million years (Table 4) for the node subtending *Unident – spartaeine* and *Portia*. The true salticids (Salticoida division) diverged from this group 31.67 million years ago. The node supporting members of the subfamily Ballinae constitutes the oldest group within the salticoida division (23.17 million years). *Padilla* diverged from this group 13.06 million years ago.

Distribution of *Padilla*

Members of the three different clades are distributed within the remnant rainforest across the northeastern and northwestern Madagascar, but only a few species are recorded from the central regions and from dry areas. The genus seems not to occur in the far south except for *P. astina* (1 specimen). It is unclear if this gap is due to lack of collections or true absence of these spiders in most of this region. But considering the intensive sampling from more than 60 sites, including places located in the far South, absence and rarity are more probable explanations. Of all the 17 localities where species of *Padilla* were collected, the evergreen montane forest of the north (Montagne d'Ambre) is the richest in species and, thus, may be considered as a zone of radiation. Many species are narrowly distributed and are known from a single locality. These localities are identified as areas of endemism for *Padilla* and are of conservation importance. They are Montagne d'Ambre and Ranomafana, both supporting two endemic species, and Lokobe, Daraina – Ampondrabe, and Itaty, each supporting one endemic species. Members of clade A have a central, southeastern, southwestern and northern distribution. Members of clade B' are distributed along the east coast, through the central region to the far north. They include the most widespread species of *Padilla* and were the only ones found in the central regions where the conditions appear less suitable. Members of clade C'; however, were mostly found in the north and northwestern Madagascar, except *P. maingoka* from the central southeastern region. They are all flattened, scorpion-like spiders with the exception of *P. foty* (Fig. 44).

Biogeography

The ballline morphology trees suggested a close relationship between *Padilla* and the genus *Philates* found in Gondwanan plates. *Philates* is known from Africa to Sri Lanka, Indonesia, Philippines, Java, Borneo, and New Guinea (Prószyński, 2006). The distribution of *Padilla* exhibits an eastern and northwestern split with a few species from the central and southern Madagascar

(Fig. 51). This seems to favor a radiation from either the East (India, Sri Lanka, Indonesia) or the northwestern part of Madagascar or northeastern Africa. The ages of *Padilla* (13.06 MYA) and the sub-family Ballinae (23.17 MYA) are too recent for Gondwanan vicariance hypothesis. According to modern understanding of the geological history of the Indian Ocean around this time frame, two other hypotheses are possible: (1) the existence of a land bridge linking Madagascar, Africa, India and the Seychelles Islands (2) transoceanic long distance dispersal. The first hypothesis suggests that as India assumed its current position from the early Eocene through Miocene, global sea levels were dropping, with a marked regression at the Rupellian/Chattian boundary (Haq et al. 1988). At that time, significant portions of the Chagos/Laccadive Plateau (about half way between Africa and Indonesia) and the contiguous Mascarene Plateau (including the Seychelles Bank), could have been emergent, and served as stepping-stones through which terrestrial organisms with low dispersal ability could migrate (Schatz 1996). Some Malagasy plants such as the genus *Pandanus* (Pandanaceae) (Martin et al. 2003), *Dillenia* (Dilleniaceae), *Nepenthes* (Nepenthaceae), Malagasy cichlid fishes (Vences et al. 2001), the gekko genus *Phelsuma*, as well as mammals, e.g., tenrecs, carnivorans, and rodents (McCalll 1997), have been suggested to have dispersed through this land bridge, also called "Lemurian stepping stones" (Schatz 1996). The second hypothesis or the long distance dispersal during the Miocene, has been suggested for Melastomaceae plants and agamid lizards (Renner 2004; Raxworthy et al. 2002), which also exhibit the same distribution and a recent divergence time as the ancestors of *Padilla*. Those organisms may have reached Madagascar by means of floating on solid materials, or transported by birds, by monsoonal winds, or by the occasional storms and cyclones that occur in the Indian Ocean and between Madagascar and Africa. I found the first hypotheses most probable in the case of *Padilla* because jumping spiders are mostly terrestrial organisms, even if the second hypotheses could also be possible.

Relationships of *Padilla* with other Salticidae

Hedin and Maddison (2003) included one balline genus in his molecular analysis of the family of Salticidae: *Pachyballus*. This genus comes out always as sister group to the genus *Mantisatta*, which in analyses with two of his genes (28S and 16S) were included within the marpissoids. Maddison expressed the concern that members of the Ballinae such as *Ballus*, *Marengo*, and similar salticids may be marpissoids. Here, I have added 15 more balline species and my phylogenetic analysis seems to suggest that members of the Ballinae may form a monophyletic group that is sister group to a large clade including marpissoids, heliophanines, freyines, euophryines, and plexipoids, as in Maddison's combined gene tree (Figs. 41–42).

Conclusion

In this study, the taxonomy and phylogenetic relationships of species of *Padilla* and the placement of this genus within the subfamily Ballinae and the family Salticidae have been assessed for the first time. The study clearly demonstrates the need for contrasting two independent phylogenies (molecular and morphology) in order to detect patterns of morphological homoplasy. For instance, it is shown that the horns, carapace height and body shape evolved convergently in *Padilla*, whereas first leg spines have proven to be more efficient in identifying some of the natural groups. It is also suggested that the most probable explanation of the horn diversification observed in this genus is sexual selection. This can be illustrated (1) by case of unusual sympatric sister species with different horn types occurring at the same locality under similar ecological parameters; (2) cases of sister species with same horn type occurring in ecologically extremely different localities and; (3) absence of correlation between horn shape and any bioclimatic variables; (4) the presence of

horns only on males when males and females have roughly the same activity and live at the same locality, and thus are probably under the same ecological pressure.

Clearly, further collections and research on *Padilla* behavior and ecology are needed to define the mechanisms of sexual selection at work and their influence on the use of horns, the diversification of body shape, and life styles.

The balline subfamily morphology analysis placed *Padilla* as a sister group of *Philates chelifer* and nested within members of the genus *Philates* (Fig. 35). Yet, the generic analysis has proved that *Padilla* was a monophyletic genus. Moreover, a well supported monophyly of the genus within the family of Salticidae has been demonstrated (Figs. 41–42). My study suggests the probable placement of *Padilla* along with other balline genera as a sister group to a large clade, including marpissoids, heliophanines, freyines, euophryines and plexipoids (Figs. 41–42).

The internal classification of the different groups within Salticidae has long been problematic (Hedin and Maddison 2001–2003, Benjamin 2004), especially, within the free embolus groups. Relationships between most of the subfamilies including Ballinae are still unresolved (Hedin and Maddison 2003). This study provides new information about the probable phylogenetic placement of a group of salticids, the subfamily Ballinae, and opens up to further molecular work on this group.

Delimitation of areas of endemism is essential to both studies of historical biogeography and conservation planning. The rarity of species of *Padilla* in tropical dry forest, their near absence in the xerophytic areas of the far south of Madagascar, and the concentration or localized distribution of species in the remaining suitable rainforest of the island, seem to indicate a sensitivity of this genus to desertification. This sensitivity must be seriously considered by those interested in conservation. Recently, due to the consequences of deforestation, the island has experienced rise of temperature and reduced rain fall that could threatened endemic species such as *Padilla* (irinnews.org on December 12, 2006).

Padilla is one of the rare beauties of nature. It is an excellent model for further evolutionary studies because of its different life styles, sexually selected characters, recent and rapid and complex speciation, which seems to be driven both by sexual and natural selection. Discovery of *Padilla* phylogeny is the first step to many phylogenetic based studies and will be of value in understanding copulatory mechanisms, sexual selection, natural selection and speciation in *Padilla* and in jumping spiders in general. Knowledge about the average rates of evolution of the 28S gene in Salticidae will be of value in future investigation of spiders' divergence times and is important in future biogeographical studies for jumping spiders.

TAXONOMY

Key to the Males

(N.B. Key to females is not provided because some species are only known from males.)

1. Horns crossing at tip (Fig. 9B) 2
   Horns not crossing at tip,; nearly straight, slightly converging towards tips, tips not close to each other (*brevis* group, *cornuta* group, Fig. 8, 9A, 7) 8
2(1) Horns basally curved inward, then outward, apically converging and crossing at tips. Distal part of chelicerae depressed. Body very compact and beetle-like (*armata* group, Fig. 10) . . . 3
   Horns basally curved outward, near apex slightly bent inward, so that the tips are close to each other (*sartor* group, Fig. 9). Body not compact and not beetle-like 6
3(2) Horns not touching at their median parts; carapace with median longitudinal light line (Figs. 10B–D) 4

Horns touching for a certain length at their median parts. Carapace lacking median longitudinal line (Fig. 10A–C) 5

4(3) Carapace divided longitudinally by thin white median line, bordered by lateral band of white scale-like setae on each lateral margin. Femur I with one large promarginal spine. Dorsum dark purple, with thin yellowish median reticulation. Body generally dark purple (Fig. 10B) ..... *Padilla griswoldi* Andriamalala, sp. nov.

Carapace divided longitudinally by thick white median line formed by scale-like setae, lacking setae on lateral margin. Femur I with two large promarginal spines. Dorsum dark brown with thick longitudinal median band of white scale like hairs. Body generally dark brown (Fig. 10D) ..... *Padilla ombimanga* Andriamalala, sp. nov.

5(3) Horns markedly bent near tips (Figs. 3E–10A) ..... *Padilla armata* Peckham and Peckham

Horns slightly bent near tips (Fig. 10C) ..... *Padilla astina* Andriamalala, sp. nov.

6(2) Tibia of first legs variable in thickness but not hook-like 7

Tibia of first legs enlarged, thick, and hook-like (Fig. 24C). Body and carapace dark brown, with two lateral, longitudinal, thin, black band on each side (Fig. 9C) ..... *Padilla maingoka* Andriamalala, sp. nov.

7(6) Carapace with red guanine deposit that includes median white spot (Fig. 3C). Tibia and metatarsus of first legs with paired symmetrical spines (of the same size on proventral and retroventral sides). Femur I with one promarginal enlarged spine. Sternum obviously wider than long. Dorsum yellowish to dark orange with medially aligned red chevrons (Fig. 9B) ..... *Padilla mazavaloha* Andriamalala, sp. nov.

Carapace with red guanine deposit, but lacking white median spot. Tibia and metatarsi of first legs with paired, obviously asymmetrical spines (of different size on proventral and retroventral sides). Femur I with two promarginal enlarged spines (Fig. 25A). Sternum obviously longer than wide. Dorsum completely dark brown, with single longitudinal yellowish band (Fig. 9A) ..... *Padilla sartor* Andriamalala, sp. nov.

8(1) Horns originating from distal part of paturon near fangs. Body flattened (CHL/ DH< 0.25); brevis group (Figs. 3G–H, 17) 9

Horns originating from proximal part of the paturon away from fangs (CHL/DH>0.50). Body not flattened (CH/ CL>0.25); cornuta group (Figs. 8B–C) 10

9(8) Horn extremely short (tooth-like), somewhat thick, and slightly convergent, originating right near fangs (Fig. 3G). Tibia swollen, with ventral tuft of black setae. Femur II-IV yellowish orange with dark lateral patches (Fig. 24B) ..... *Padilla boritandroka* Andriamalala, sp. nov.

Horn as long as one-third of carapace, directed downwards, slender, originating just above fangs (slightly higher than in of *P. boritandroka*; Fig. 3H). Femur II–IV uniformly yellowish orange (Fig. 17B) ..... *Padilla ngeroka* Andriamalala, sp. nov.

10(8) Carapace dorsally with white, medially constricted guanine deposit. Dorsum of abdomen yellowish, with a pair of thick, lateral, dark bands (Fig. 8A) ..... *Padilla cornuta* Simon.

Carapace dorsally without white guanine deposit. Dorsum of abdomen rather dark, with sclerotized scutum that may be covered with stripes of green iridescent scales. (Figs. 8B–C) .. 11

11(10) Tibial spur present (Fig. 25B). Carapace and abdomen dark, with horizontal stripes of green iridescent setae. Legs II–IV uniformly yellowish orange (Fig. 8B) ..... *Padilla manjelatra* Andriamalala, sp. nov.

Tibial spur absent. Carapace and abdomen mottled dark and light brown, without setal stripes. Abdomen with dark brown scutum which sometimes shows yellowish reticulation. Legs II–IV dark brown, with black horizontal stripes (Fig. 8C) ..... *Padilla lavatandroka* Andriamalala, sp. nov.

Genus *Padilla* Peckham and Peckham 1894

Padilla Peckham and Peckham 1894, Proc. Nat. Hist. Soc. Wisconsin 2:130 (type species, by monotypy, *P. armata* Peckham and Peckham 1894, deposited in MCZ, Havard, type number 117, examined). Simon 1900, Ann. Soc. Ent. Belg: 395. Simon 1901, Histoire Naturelle des Araignées 2:472.

The genus *Padilla* is correctly placed within the subfamily Ballinae. All species have the characteristics of this subfamily, as follows:

(1) Embolus laying flat on the tegulum that coils at least 360 degrees (Maddison 1988, 1995; Benjamin 2004). In *Padilla* the embolic coil is always with two spirals (Figs. 29, 31–33).
(2) Tegulum divided by a pale longitudinal furrow and a subtegulum extending posteriorly beyond cymbium (Maddison 1995, 1996; Benjamin, 2004). In *Padilla*, the tegulum division may also be an invagination or an abrupt hole that is generally located quite medially as opposed to laterally, e.g., in *P. griswoldi* (Fig. 33B), on the side of the palp in other balline genera.
(3) Palp simple, lacking pars pendula, conductor and median apophysis (Benjamin 2004).
(4) Epigynum with a narrow septum (ek) and with copulatory openings (co), fertilization ducts (fd) and spermathecae (spc) in a linear arrangement (Fig. 26) as observed in some but not all balline genera (Benjamin 2004).
(5) Femur of the first leg generally enlarged (Benjamin 2004). In *Padilla*, femora of the first legs always enlarged.

Diagnosis.— *Padilla* can be differentiated from other genera of the Ballinae by the following combination of characters:

(1) The presence of a pair of horns or forward projecting processes on the male chelicerae.
(2) Femora of leg III and IV with a linear arrangement of three dorsal spines (1/1/1) (Fig. 25D).
(3) Femur and patella of first legs with a fringe of setae along dorsal side.
(4) Path of the sperm duct intermediate between C and S (rather C or S in other balline genera) (Fig. 2C).

All *Padilla* except *P. foty* are also unique in having a serrula (or endite ridge) extending till the base of the endites (Fig. 30D).

Note.— Possible synapomorphies for the genus are the presence of a pair of horns on the male chelicerae, presence of fringe of setae along the retromarginal dorsal side of femora and patella of leg I, and path of the sperm duct intermediate between C and S.

Relationship with members of subfamily Ballinae.— Within the Ballinae, no known genera have horn like projections on the male chelicerae. Although *Goleta workmani* (Peckham and Peckham 1884) has a short spine-like projection on the male chelicerae that is quite similar to one *Padilla* (*Padilla boritandroka*), it was excluded from the Ballinae due to a lack of the diagnostic characters of this subfamily (Benjamin 2004) and presents a completely different palp structure compared with all the balline genera. Some balline species, such as *Cynapes wrightii, Colaxes nitidiventris* and *C. wanlessi, Ballus segmentatus* and *B. chalybeius*, *Philates chelifer* and *P. grammicus, Indomarengo sarawakensis* and *I. chandra,* and *Sadies fulgida,* share with *Padilla* an embolic coil with one or two spirals. However, the two species of *Indomarengo* have a prosomal protuberance (pp) on the posterior part of their carapace (Benjamin 2004, Fig. 55) and posterior median eyes (PME) larger than anterior lateral eyes (ALE). Those characters are not present in any of the *Padilla*. *Ballus segmentatus*, *B. chalybeius* and *Cynapes wrightii* all have a broader epigynal septum (Figs. 9, 18, 22, 23 in Benjamin 2004). *Ballus segmentatus* also has a different spine arrangement on femur III and IV (Alicata and Cantarella 1987). *Philates* is the closest to *Padilla* morphologically. However, *Philates* lacks the male cheliceral horns and has long and large leaf like scales

on Tb1 which were not observed in any of the *Padilla* (Fig. 52C). In addition, the path of the sperm duct is C instead of intermediate between C and S as in *Padilla* (Fig. 2).

Description.— *Padilla* are small sized salticids with a total length of 4.31–6.93 in ♂, 4.72–6.93 in ♀. A ratio of measurements between various parts of the body and a measure of some parameters are reported in Table 1. The specimens available do not form an adequate statistical sample, but one can obtain at least an idea of intraspecies variation and of the differences and similarities between species.

Padilla are sexually dimorphic. Males and females are quite different , the differences being more or less pronounced depending on the species. For example, in *P. ngeroka* males and females display completely different coloration and markings. The male is completely dark, whereas the females are rather yellowish with two lateral dark bands. Females of *P. manjelatra* and *P. lavatandroka* also have different leg coloration compared with their males. However, males and females of some species, such as *P. mazavaloha* and *P. cornuta,* are very similar except for the presence of secondary sexual traits such as the horns and the tibial spurs, which are absent in females. The dimorphism is expressed more in body coloration and the secondary sex traits such as leg spination and the presence of cheliceral horns, rather than body size. This is often the case in hunting spiders where both male and female exhibit the same feeding activities (Alroth 1995).

The presence of horns originating from the upper (proximal) or lower (apical) part of the male chelicerae is one of the synapomorphies that unite all species of *Padilla*. These horns may range from being as long as the carapace to extremely short as a spine (Fig. 3G). I divided the male *Padilla* in four separate groups according to (1) origin and curvature of these horns and (2) on phenetic similarity in carapace shape (implying "runner" or "hopper" lifestyle): the *sartor* group, *cornuta* group, *armata* group and *brevis* group. The *sartor* group is characterized by horns dorsally presenting a simple curve, as opposed to horns that present a double curve in *armata group* (Figs. 3C–D, 9). Within the *cornuta* group and the *brevis* group, the horns are rather straight and convergent (Figs. 3A–G). In this latter group, the horns originate from the distal part of the chelicerae. Three species that are known only from females were left unassigned. I find these groups very useful for communicating about *Padilla*. [List of these species groups is given in appendix 1 and their monophyly tested with morphology and molecular data in the phylogenetics section above.

Sartor group: males within this group have horns that originate from the proximal part of the chelicerae and which curve first outwards, then inwards, finally crossing each other at their apex (Figs. 3C–D, 9); in *P. sartor* the horns meet but do not cross (Fig. 9A). The tegulum division of the palp is a shallow invagination instead of a groove (Figs. 31D-E-G-H). The species that are included within this group are: *P. sartor, P. mazavaloha,* and *P. maingoka.*

Armata group: All males within this group have horns that originate from the proximal part of the chelicerae and which curve first inwards, and may be distant from, close to, or touching each other. The horns then go outwards, and finally curve inwards and cross at their tips (Figs. 3E–F, 10). The palp has a tegulum with a deep groove and a ventral posterior knob (Figs. 33B-D-H). The species that are included within this group are: *P. armata, P. griswoldi, P. astina,* and *P. ombimanga.*

Cornuta group: All males within this group have straight and convergent horns that originate from the proximal part of the chelicerae (Figs. 3A–B, 8). The palp has the tegulum with a shallow tegular groove (Figs. 29E–H). The species that are included within this group are: *P. cornuta, P. manjelatra,* and *P. lavatandroka.*

Brevis group: All males within this group have horns that originate from the distal part of the chelicerae and which are straight (Figs. 3G–H). The chelicerae project forward and are parallel to the carapace instead of perpendicular to it (Fig. 3H); the paturons are flattened dorsally with pro-

marginal and retromarginal sharpened edges (Figs. 14D–E). The palp has an embolus coil (ec) that is inclined toward the retrolateral side, with embolus second loop (el) thickened and embolus fold (ef) present on the prolateral side. The tegulum division (tg) is a shallow invagination (Fig. 32). The species that are included within this group are: *P. boritandroka* and *P. ngeroka.*

General description of Padilla.— Carapace generally smooth (Figs. 53A–C), with length 1.63–3.1 in ♂, 1.96–3.33 in ♀, and varies in height and width (Figs. 3, 28), with cephalothorax height 1.33–0.44; cephalothorax width 0.88–2.63. The higher the carapace, the wider the region between leg II and III. Carapace almost rectangular (Fig. 9C) in the most flattened species (*P. maingoka*), whereas trapezoidal and greatly enlarged between leg II and III (Figs. 3A, 4A, 8B–C) in males of *P. manjelatra* and *P. lavatandroka*. Top of carapace often decorated with differently colored and shaped guanine deposits (Fig. 3C, 10, 16): usually red in the *sartor* group (except *P. maingoka*) (Fig. 9A–B), orange in some members of the *armata* group (Figs. 10B–C), white with a median constriction in *P. cornuta* (Figs. 5, 8A), and unicolor in some species, i.e., *P. manjelatra* (Figs. 6, 8B), and *P. maingoka* (Figs. 9C, 23). In some species, bands of white scales present on lateral sides of carapace and above clypeus (Figs. 12C, 53B–D); bands particularly thick in *P. mihaingo* (Fig. 27B). Cephalic region shorter than thoracic (Simon 1900). Ocular quadrangle as wide anteriorly as posteriorly, W.O.F I 0.76–2.06, W.O.F II 0.95–1.96. Eyes surrounded by black pigmentation (Fig. 3C-E-F-G), PME twice as large as ALE, PME small, PLE not raised except in *P. lavatandroka* and *P. manjelatra.* Thoracic fovea either point like (3E), or short line (Figs. 3C, 54F), or shallow invagination (3A). Clypeus generally low; chilum present or absent (Fig. 14C). Chelicerae may be strong thick, or elongate, or conspicuous in the ♂ of some species (all *armata* group, all *sartor* group except *P. maingoka,* generally all *cornuta* group) and slender in some other ♂ such as *P. maingoka*, ♂ within *brevis* group and generally in ♀. The edge of paturon either carinate *(brevis* group, all male *armata* group*)* or not. Distal part of paturons either depressed (*Armata* group) or not. Fangs generally short and thick (Fig. 14). Promargins of chelicerae usually pluridentate with three to five teeth continued with sharp line, whereas the retromargins vary from fissidentate to pluridentate depending on species (Fig. 30C). The number of teeth or points (for fissidentate) varies from 4 to 6. Endites generally flattened and sometimes sclerotized, elongated and parallel-sided in some species, rather apically expanded in some others (Fig. 30B). Labium generally flattened, longer than wide and sclerotized (Fig. 30B). Sternum either flattened or convex, generally longer than wide, with broad (Fig. 30A), truncated or narrow anterior margin.

Leg formula 1432. First legs longer and larger than other legs. Femora of first legs usually with two or three bristles on dorsal surface, two or three prolateral spines, and one or two proventral spines (Fig. 24, 25A). Tibia of first leg as wide as or wider than femur, with three pairs of spines that may be symmetrical (Figs. 24B–D) or asymmetrical (Figs. 24A–C), with fringe of thick setae on ventral side in some species (*P. boritandroka;* Fig. 24B), either simple or hook-like (*P. maingoka*; Fig. 24C). Metatarsus of first leg without a preening comb; bearing two pairs of spines on ventral surface that may be symmetrical (of the same size on proventral and retroventral surfaces) or not (*armata* group); metatarsus pseudosegmented or curved in a*rmata* group; ventral surface of metatarsus of some species withdark spot that may extend longitudinally between two metatarsal spines. Tarsi with two pectinate claws with different numbers of teeth as in all members of the Salticoida division (Maddison, 2003), e.g., prolateral claw with 23 teeth, retrolateral with 11 teeth; claw tuft usually black, scopulae absent (Fig. 52D–E). Femora of legs III–IV often with row of three dorsal spines (1/1/1), with additional proventral distal spine or retroventral distal spine, or both, depending on species (Fig. 25D). Metatarsus of leg III often with long trichobothrium on dorsal side. Abdomen with scutum in *P. lavatandroka* and *P. boritandroka* (Figs. 7, 55). Some species of *cornuta* and *armata* groups have two or three pairs of dark patches on abdominal dorsum (Figs. 7,

20). Spinnerets may be preceded by plate. Anterolateral spinnerets (ALS) often conical, sometimes cylindrical, and shorter than the posterolaterals (PLS). ALS of ♀ with several pyriform gland spigots and two major ampullate gland spigots (MAP) on mesal margin. ♂ ALS with only one MAP. Both ♂ and ♀ PMS show two classes of spigots: two minor ampullate gland spigots (mAP) located medially, and three aciniform gland spigots (AC). ♀ PLS with with seventeen AC; ♂ PLS with fifteen AC (Fig. 56). Cylindrical gland spigots absent, often the case of spiders that lay eggs within a retreat and cover them with layers of silk threads (Kovoor 1979). Details of male palp and female epigynum discussed above and below in species descriptions.

Natural History.— Nearly all species of *Padilla* for which collection data are available have been collected either by beating low vegetation, from pitfall traps or rarely from Malaise traps in humid tropical high or low altitude forests. The majority of species occur in warm and wet areas where the annual mean temperature varies between 15.9°C and 26.3°C and the mean annual precipitation is 367–1829 mm (Table 5), however, a few species were collected from tropical dry forest (*P. mihaingo, P. mitohy*). The genus was mostly found along the eastern north and northwestern evergreen forests and central mountain rain forests at 700–1300 m elevation. Species of *Padilla* were located between 10–1300 m elevations, however, the "runners" were mostly found below 780 m in deciduous broadleaf low altitude forest, shrubland or wooded grassland, except *P. maingoka* (900 m). *Padilla* was almost absent in the far South where the vegetation is xerophytic except *P. astina*, which was collected from a dry spiny forest near the beach. Many species were concentrated in the evergreen mountain rain forest of Montagne d'Ambre. Several species are narrowly distributed, e.g., *P. griswoldi, P. astina, P. foty, P. maingoka,* and *P. mihaingo* were only collected from one locality. The genus seems to be very rare. Despite the intensive collecting from more than 60 sites of varied vegetation and altitude across the island, only 107 specimens were collected (including adults and juveniles).

Composition.— Fifteen species are presented here in this study, including the three previously described species, *Padilla armata* Peckham and Peckham, 1894, *P. cornuta* (Peckham and Peckham, 1885), and *P. sartor* Simon, 1900, and twelve newly described.

The types of three other species, *P. mantis* Simon, 1900, *P. glauca* Simon, 1900 and *P. lancearea* Simon, 1900, all described from Madagascar, could not be located and are considered lost. These names are considered *nomina dubia*. I also exclude *P. javana* (Java) from the genus because it lacks the horns on male chelicerae, a diagnostic character of *Padilla*, (Prószyński, 2003 in *Padilla*: <*http://salticidae.org/salticid/diagnost/padilla/padilla.htm*>).

Distribution.— Probably all of Madagascar except the far South (Figs. 51, 57, 58, 59).

Padilla armata Peckham and Peckham, 1894

Figs. 3E, 4B, 10A, 12A, 18.

Padilla armata Peckham and Peckham, 1894:130–132, pl. 13, fig. 1 (Syntypes from Madagascar, no specific locality, deposited in MCZ, Harvard, type number 117, examined). Simon, 1901a: 472, f. 542. Prószyński, 1984a: 95. Wanless and Lubin, 1986: 1211, f. 3A, C. Platnick, 2006.

Material examined.— Syntypes. Madagascar: no specific locality, 1894, Peckham and Peckham, 1♂ 8 juveniles deposited in MCZ, Harvard, type number 117.

Lectotype designation.— The one adult male is here designated as the lectotype.

Diagnosis of the *armata* group.— Distinguished from other male *Padilla* in having (1) horns dorsally presenting a double curve, first going inward, then outward, finally converging and crossed at the tips, about as long as half of the carapace length (horn length/carapace length: 0.51–0.67), originating from the proximal part of the chelicerae, and either distant from, or close

to, or touching each other (Figs. 10B, 12B, 18), (2) tibia of first legs with spines that are only present on proventral surface, retroventral surface without spines (unpaired; Fig. 24A), and consist of one larger distal and two smaller proximals (asymmetrical), (3) body very compact and beetle-like (Figs. 18, 10B), (4) abdomen almost as long as the carapace and (5) lateral margins of the paturons carinate.

Diagnosis.— *P. armata* can be distinguished from all other males within the *armata group* by the following combination of characters: (1) horns sharply bent near the distal end (not sharply bent in *P. astina*), touching each other at their median parts (as in *P. astina*, but different from *P. griswoldi*) (Fig. 3E), (2) abdomen somewhat longer and heavier compared with the cephalothorax (somewhat shorter in *P. astina* and *P. griswoldi*; Fig. 12) and (3) carapace guanine deposit very pale.

Description.— Male (Lectotype, no specific locality): Carapace reddish orange with two dark patches anteriorly, abdomen yellowish orange with an orange scapus, with aligned dark brown patches separated by yellowish white setae in juveniles female. Legs orange, darkened at their promargins; all eyes surrounded by dark pigmentation (Figs. 3E, 4B, 18).

Total length: 5.88. Carapace length: 2.63. Abdomen length: 3.25. Horn length/carapace length: 0.61. Horn width: 0.21. DH: 0.50. DH/CHL: 0.75. Width ocular field I: 1.33. Width ocular field III: 1.36. Height cephalothorax: 0.80. Diameter AME/length chelicerae: 0.61. Height cephalothorax/width cephalothorax: 0.42. Width cephalothorax/width ocular field III: 1.40.

Femur I/width ocular field II: 1.44. Femur III/width ocular field III: 0.85. Femur IV/Femur III: 1.10. Tibia I/width ocular field III: 1.07. Tarsi I/metatarsi I: 0.34.

Promargins of chelicerae pluridentate, with five teeth and continued distally as sharp line; retromargins fissidentate with six points.

Natural history.— Not specified by Peckham and Peckham (1894).

Distribution.— Peckham and Peckham (1894) did not specify where in Madagascar the type specimens of *Padilla armata* were collected.

***Padilla griswoldi* Andriamalala, sp. nov.**
Figures 10B, 12B, 19, 25D, 33A–C, 60–61.

Material examined.— Holotype: Madagascar: **Fianarantsoa Province:** Ranomafana National Park, 1500 m, 21.2554°S, 47.4552°E, rainforest, Malaise trap, 12–21 December 1999, E.I. Schlinger and M.E. Irwin, 1♂ (CAS), CASENT 9021858. Other material examined: Madagascar: **Fianarantsoa Province:** Ranomafana National Park, radio tower, 1300 m, 21.25083°S 47.4071713°E, rainforest, Malaise trap, 3 December 2002, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9021902.

Etymology.— The species name is a patronym in honor of my advisor, Charles E. Griswold.

Diagnosis.— *Padilla griswoldi* differs from other *Padilla* of the *armata* group in having the following characters: (1) carapace divided by a thin longitudinal white line, (2) horns convergent, close to but not touching each other at their median part (as it is in *P. astina*), then going outward before slightly crossing near tips, bases widely separated (very close to each other in *P. astina*), (3) guanine deposit extending towards the posterior part of the carapace (Figs. 10B,19), (4) horns cylindrical, sharpened and darkened on their margins, with rows of setae on lateral edges, and stridulating lines on dorsal and ventral sides, mostly near the tips and (5) femur III dorsally without additional retromarginal spine (Fig. 25D).

Description.— Male (Holotype from Ranomafana National Park, Fianarantsoa, Madagascar): Carapace brown reddish with red guanine deposit, thin white median line, and one thick lateral band of white scales on each side. Margin of clypeus with fringe of white scales. Abdomen reddish brown with thin yellowish median folium (Fig. 19). Legs brown, darkened on their promarginal and retromarginal sides (Fig. 19).

Total length: 5.39. Carapace length: 2.46. Abdomen length: 2.93. Horn length/carapace length: 0.51. Horn width: 0.18. DH: 0.58. DH/CHL: 0.97. Width ocular field I: 0.76. Width ocular field III: 0.76. Height cephalothorax: 0.44. Diameter AME/length chelicerae: 0.81. Height cephalothorax/width cephalothorax: 0.24. Width cephalothorax/width ocular field III: 2.41.

Femur I/width ocular field III: 2.16. Femur III/width ocular field III: 1.16. Femur IV/Femur III: 1.34. Tibia I/width ocular field III: 1.79. Tarsi I/metatarsi I: 0.51.

Promargins of the chelicerae pluridentate with three teeth. Retromargins fissidentate with five teeth.

Variation.— Male (n=2): carapace length: 2.33–2.46. Abdomen length: 2.93–3.06. Diameter AME: 0.38–0.40. Horn length/ carapace length: 0.51–0.56. Femur I length: 1.64–1.66.

Female: Unknown.

Natural history.— Specimens were collected from rainforest in Malaise traps.

Distribution.— Central Southern Madagascar (Fig. 60, 61).

***Padilla astina* Andriamalala, sp. nov.**

Figures 10C, 12C, 14C, 20, 24A, 33D–F, 60–61.

Material examined.— Holotype: Madagascar: **Toliara Province**: Ifaty 18 km N of Toliara, 20 m, 23.1885°S 43.6239°E, tropical dry forest, malaise trap, 14 December 1999, E.I. Schlinger, 1♂ (CAS), CASENT9021860.

Etymology.— The species name is taken from Astina, my mother's name.

Diagnosis.— Distinguished from *Padilla griswoldi* in having the following characters: (1) carapace without a longitudinal median white line, (2) guanine deposit not extending towards the posterior part of the carapace, restricted to its anterior parts, (3) horns not sharply bent near the distal end (different from *P. armata)*, convergent, touching each other for a certain distance at their median part, then continuing outwards before conspicuously crossing at their tips, (4) horn bases very close to each other and (5) femur III with an additional distal retromarginal spine (Fig. 10C, 20).

Description.— Male (Holotype from Ifaty, Toliara, Madagascar): Carapace with two anterior dark spots of guanine deposit and thick lateral band of white scales. Clypeal margin with fringe of white scales (Fig. 14C). Abdominal dorsum with two pairs of dark yellowish patches and a wide yellowish median band, followed laterally by narrow reddish brown bands. Spinnerets preceded by thin, wide yellowish plate. Legs brown, darkened on their promarginal and retromarginal sides, same as in *P. griswoldi* (Fig. 20).

Total length: 4.69. Carapace length: 2.13. Abdomen lenght: 2.56. Horn length/carapace length: 0.67. Horn width: 0.18. DH: 0.44. DH/CHL: 0.92. Width ocular field I: 1.16. Width ocular field III: 1.13. Height cephalothorax: 0.71. Diameter AME/length chelicerae: 0.83. Height cephalothorax/width cephalothorax: 0.44. Width cephalothorax/width ocular field III: 1.44.

Femur I/ width ocular field III: 1.38. Femur III/width ocular field III: 0.76. Femur IV/Femur III: 1.16. Tibia I/width ocular field III: 1.12. Tarsi I/metatarsi I: 0.45.

Promargins of the chelicerae pluridentate, with three distal teeth and a proximal sharp line; retromargins fissidentate with four points.

Female: Unknown.

Natural history.— Specimen was collected from tropical dry forest by Malaise trap.

Distribution.— Southern Madagascar (Figs. 60, 61)

***Padilla ombimanga* Andriamalala, sp. nov.**

Fig. 10D, 12D, 21, 33G-H-I, 47, 48.

Material examined.— Holotype: Madagascar: **Antsiranana Province**: Park National Montagne d'Ambre, 1000–1200 m, 12°31′53.5″S; 49°10′36.8″E , tropical rainforest, beating trees, 14-20 December 2005, Hannah Wood and Harisoa Raholiarisendra, 1♂ (CAS), CASENT9023432.

Etymology.— The species name is from the Malagasy "*ombimanga*," which refers to a "black bull."

Diagnosis.— Distinguished from *P. griswoldi* and *P. astina* by the following characters: (1) carapace without a thick band of white scales on lateral sides, (2) femur of leg I with two proventral spines (as in *P. sartor*, Fig. 25A), (3) abdomen with a single median band of thick white scales that is extended horizontally at the posterior part, (4) clypeus without a thick fringe of white scales, (5) horns very close to each other, but not touching and (6) horn bases very close to each other and not widely separated (Figs. 10D, 21).

Description.—Male (Holotype from National Park Montagne d'Ambre, Antsiranana, Madagascar): Carapace dark brown with an orange thin horizontal guanine deposit along the anterior edge. Clypeal margin without a fringe of white scales. Abdominal dorsum dark brown with a single thick longitudinal band of white scales. Three pairs of dark patches are visible on the dorsum. First legs dark brown; all the other legs yellow. Spinnerets not preceded with a plate (Fig. 21).

Total length: 5.92. Carapace length: 2.76. Abdomen length: 3.16. Horn length /carapace length: 0.61. Horn width: 0.23. DH: 0.7. DH/CHL: 0.8. Width ocular field I: 1.5. Width ocular field III: 1.53. Height cephalothorax: 0.84. Diameter AME/length chelicerae: 0.73. Height cephalothorax/width cephalothorax: 0.30. Width cephalothorax/width ocular field III: 1.41.

Femur I/width ocular field III: 1.38. Femur III/width ocular field III: 0.759. Femur IV/Femur III: 1.21. Tibia I/width ocular field III: 1.21. Tarsi I/metatarsi I: 0.446.

Promargins of the chelicerae are pluridentate with five teeth and a distal sharp line. Retromargins are fissidentate with five teeth.

Female: Unknown.

Natural history.— Specimen was collected from tropical dry forest by beating trees.

Distribution.— Northern Madagascar (Figs. 47, 48).

***Padilla sartor* Simon, 1900**

Figs. 9A, 16, 15A, 25A, 31A–C, 47–48.

*Padilla sarto*r Simon, 1900b:393 (type specimen from Madagascar (no specific locality given), not located in MNHN Paris, not examined); Simon, 1901a: 461, f. 539–541 (m); J. Prószyński 2000, Platnick 2006.

Material examined.— Madagascar: **Antsiranana Province**: National Park Montagne d'Ambre, 12.2km 211° SSW of Joffreville, 1300 m, 12°35′47″S, 49°9′34″E, mountain rainforest, beating low vegetation, 2–7 February 2001, Fisher/Griswold Arthropod Survey team, 1♂ (CAS), CASENT 9021839.

Note.— The type specimen of *Padilla sartor* was not located, and seems to be lost. However, the drawings of the diagnostic characters from Simon's 1900 original description (also shown in "Diagnostic, Drawing Library" by Prószyński 2000) correspond to the characteristics of a male specimen collected from Montagne d'Ambre (Northern Madagascar) by the following characters: (1) horn curving outward then inward with tips separated and (2) femur of leg I with two proventral strong spines (Fig. 25A). Even though there are some slight differences between the specimen observed and Simon's descriptions (concerning the abdomen coloration, presence of bands of scales on the margins of the carapace and geographic location), I will consider and describe here this specimen as *Padilla sartor* until the type and additional specimens are observed.

Diagnosis of the *sartor* group.— Distinguished from other male *Padilla* not included in the *Sartor* group by having (1) a pair of horns projecting forward from the proximal parts of the chelicerae, which, dorsally, first curve outward, and distally slightly bend inward, so that the tips are close to or crossing each other, laterally going upward with tips exceeding the middle of AME (Figs. 3C–D); (2) a red guanine deposit on the ocular area of the carapace, except for *P. maingoka* (Figs. 9, 16, 22, 23) and (3) tegulum division of the palp is a shallow invagination instead of a groove (Figs. 31D–E-G–H).

Diagnosis of *P. sartor*.— Distinguished from all other males within the *Sartor* group by the following combination of characters: (1) horns as long as half of the carapace (horn length/carapace length: 0.5), with the tips not crossed (different from *P. mazavaloha* and *P. maingoka*), (2) femur of leg I with two proventral strong spines (only one in *P. mazavaloha* and *P. maingoka*) (Fig. 25A), (3) abdomen dark with a single longitudinal yellowish band (with longitudinally aligned chevrons in *P. mazavaloha*), (4) guanine deposit only red (red with a white median part in *P. mazavaloha*), (5) tibia I without a promarginal spur (present in *P. mazavaloha*), (6) tibia and metatarsi I with asymmetrical pairs of spines on pro and retroventral sides (spines are of different size on pro and retroventral sides) and (7) male palp with embolus base concave, posterior part of the tegulum visible, and tegulum division a shallow invagination (Figs. 31A–C).

Description.— Male (from Montagne d'Ambre, Antsiranana, Madagascar): Carapace dark brown with red guanine deposit and two black spots on top; abdomen dark brown with a single yellowish longitudinal band; all eyes surrounded by dark pigmentation; first legs dark brown, other legs yellow (Figs. 9A, 16).

Total length: 5.76. Carapace length: 2.60. Abdomen length: 3.16. Horn length/carapace length: 0.50. Horn width: 0.24. DH: 0.40. DH/CHL: 0.66. Width ocular field I: 1.53. Width ocular field III: 1.50. Height cephalothorax: 0.80. Diameter AME/length chelicerae: 0.86. Height cephalothorax/width cephalothorax: 0.53. Width cephalothorax/width ocular field III: 1.44.

Femur I/width ocular field III: 1.36. Femur III/width ocular field III: 0.83. Femur IV/Femur III: 1.13. Tibia I/width ocular field III: 1.20. Tarsi I/metatarsi I: 0.47.

Promargins of chelicerae pluridentate with five teeth and continued distally with a sharp line; retromargins are fissidentate with six points.

Female: Unknown.

Natural history.— A specimen was collected from mountain forest by beating low vegetation.

Distribution.— Northern and eastern Madagascar (Figs. 47–48). The type specimen was collected from Tamatave, Sainte-Marie (Toamasina Province), whereas the one male specimen described above was collected from Montagne d'Ambre (Antsiranana Province).

***Padilla mazavaloha* Andriamalala, sp. nov.**
Figures 3C, 4Ca, 9B, 15B, 22, 31D–F, 52B, 53A.

Material examined.— Male holotype and female paratype: Madagascar: **Antsiranana Province:** National Park Montagne d'Ambre, 3.6 km 235° SW of Joffreville, 925 m, 12°32′4″S, 49°10′46″E, mountain rainforest, beating low vegetation, 20–26 January 2001, Fisher/Griswold Arthropod Survey team, 1♂ 1♀(CAS), CASENT 9006683. Other material examined.— Madagascar: **Antsiranana Province:** National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000 m, 12°32′S, 49°10′E, 21–30 May 1993, Fisher/Griswold Arthropod team: 1♂ 3♀ (CAS), CASENT9021899 – 4♀ (CAS), CASENT9020188. National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000–1200 m, 12°31′53.5″S, 49°10′36.8″E, 14–20 December 2005, Fisher/Griswold Arthropod team: 1♀ (CAS), CASENT9023433 – 1♀ (CAS), CASENT9023434 – 1♀ (CAS), CASENT9023435. National Park Montagne d'Ambre, 3.6 km 235°

SW Joffreville, 925m, 12°32′4″S, 49° 10′46″E, 20–26 January 2001, L.J. Boutin coll, 1♀ (CAS), CASENT9000755. Reserve Speciale Manongarivo, 10.8 km 229° SW Antanambao, 400 m, 13°577′S, 48°26′E, 8 May 1998, B.L. Fisher, 6♀ (CAS), CASENT9020185. **Fianarantsoa Province:** National Park Ranomafana, radio tower, 1130 m, 21.25083°S, 47.40717°E, 3 September 2003, R. Harin'Hala, 1♂(CAS), CASENT 9006891.

Etymology.— The species name is from the Malagasy word "mazava loha," which refers to a dark zebu bull with a clear yellowish head.

Diagnosis.— Distinguished from *P. sartor* and *P. maingoka* by the following combinations of characters: (1) guanine deposit on the ocular area is red, but with a median white spot (Figs. 3C, 4Ca), (2) abdominal dorsum with chevrons on the posteromedian instead of a single yellowish median band (Figs. 9B, 22), (3) tibia I provided with a distal proximoventral spur (same as in *P. cornuta* in Fig. 25C) and (4) tibia and metatarsus I with symmetrical pairs of spines (spines of the same size on pro and retroventral sides). Also, metatarsus I has a ventral black spot extending over space between the two metatarsal spines. Sternum is broader than long.

Description.— Females and males are of the same color (yellowish to orange), but males are a bit darker. Carapace yellowish, slightly darker at the anterolateral regions (dark brown in males and brown orange in the posteromedian); abdomen yellowish, with two dark longitudinal lateral bands and median chevrons in females; dark with median chevrons in males; all eyes surrounded by dark pigmentation; first legs yellowish, and slightly darkened on the pro and retrolateral sides (completely dark, except for the tarsi in males), all other legs yellow (Fig. 22).

MALE (Holotype from National Park Montagne d'Ambre, Antsiranana, Madagascar): Total length: 5.22. Carapace length: 2.46. Abdomen length: 2.76. Horn length/carapace length: 0.42. Horn width: 0.32. DH: 0.56. DH/CHL: 0.82. Width ocular field I: 1.46. Width ocular field III: 1.45. Height cephalothorax: 0.76. Diameter AME/length chelicerae: 0.84. Height cephalothorax/width cephalothorax: 0.53. Width cephalothorax/width ocular field III: 1.28.

Femur I/width ocular field III: 0.97. Femur III/width ocular field III: 0.69. Femur IV/Femur III: 1.16. Tibia I/width ocular field III: 0.83. Tarsi I/metatarsi I: 0.51.

Promargins of chelicerae pluridentate with three teeth and a distal sharp line, retromargins fissidentate with six points.

Variation.— Male (n=2): total length: 5.23–5.56. Carapace length: 2.46–2.70. Abdomen length: 2.76–2.86. Femur I length: 1.40–2.02.

Female (Paratype from National Park Montagne d'Ambre, Antsiranana, Madagascar): As male but without promarginal distal spur on tibia I.

Total length: 5.39. Carapace length: 2.26. Cephalothorax width: 1.65. Width ocular field I: 1.40. Width ocular field III: 1.33. Height cephalothorax: 0.72.

Tibia I/width ocular field III: 0.78. Tibia III/tibia IV: 0.64. Patella III/tibia III: 0.96. Femur I/width ocular field III: 1.09. Femur III/width ocular field III: 0.75.

Promargins of chelicerae pluridentate with six teeth, retromargins fissidentate with six points.

Variation.— Female (n=5): total length: 4.72–5.76. Carapace length: 2.16–2.33. Abdomen length: 2.56–3.43. Cephalothorax width: 0.88–1.73. Femur I length: 1.24–1.46. Patella III/tibia III: 0.86–1.25.

Natural history.— Specimens were collected from mountain forest or in rainforest by beating low vegetation between 400–1130 m elevations. The localities where the species were found have an annual mean temperature which varies between 18°C and 24°C, and a precipitation up to 809–1142 mm during the rainy season, 48–123 mm during about the four months dry season (Worldclim version 1.3).

Distribution.— Widespread in northern and eastern Madagascar.

***Padilla maingoka* Andriamalala, sp. nov.**
Figures 9C, 14A, 15C, 23, 24C, 28C, 31G–I.

MATERIAL EXAMINED.— HOLOTYPE: MADAGASCAR: **Fianarantsoa Province:** Ranomafana National Park, Talatakely, 900 m, 21.25041°S 47.41945°E, 10–16 January 2001, D.H Kavanaugh, K.M. Kavanaugh, R. Brett, E. Elsom and F. Vargas, 1♂ (CAS), CASENT 9003529. OTHER MATERIAL EXAMINED: same locality as holotype, 2–22 January 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT 9003506.

ETYMOLOGY.— The species name is from the Malagasy word "Maingoka," which means "scorpion".

DIAGNOSIS.— Differs from all males within the *Sartor* group by the following combination of characters, (1) tibia I hook like (Fig. 24C), (2) body flattened and more convex (protruding for *P. sartor* and *P. mazavaloha*) (Figs. 15C, 28C), (3) horns shorter (horn length/ carapace length: 0.38), tips crossed at the apex, weakly separated from each other, (4) carapace ocular area with a faint yellowish guanine deposit instead of red, or guanine deposit absent and (5) femur III with additional promarginal spine (three dorsal spines only in *P. sartor* and *P. mazavaloha*). Metatarsi without ventral black spot extending over space between the two metatarsal spines.

DESCRIPTION.— MALE (Holotype from Talatakely, Ranomafana National Park, Fianarantsoa, Madagasacar): Carapace and abdomen dark brown with two thin dark longitudinal lines on lateral sides; anterior part of carapace ocular area bears a faint horizontal yellowish guanine deposit; all eyes surrounded by dark pigmentation; first legs brown, darker on pro and retrolateral sides, other legs yellowish (Fig. 23).

Total length: 6.09. Carapace length: 2.56. Abdomen length: 3.53. Horn length/carapace length: 0.38. Horn width: 0.12. DH: 0.38. DH/CHL: 0.90. Width ocular field I: 1.28. Width ocular field III: 1.30. Height cephalothorax: 0.66. Diameter AME/length chelicerae: 0.95. Height cephalothorax/width cephalothorax: 0.39. Width cephalothorax/width ocular field III: 1.30.

Femur I/ width ocular field III: 1.46. Femur III/width ocular field III: 0.63. Femur IV/Femur III: 1.36. Tibia I/ width ocular field III: 1.26. Tarsi I/metatarsi I: 0.41.

Promargins of chelicerae with three teeth and a distal sharp line, retromargins fissidentate with five points.

VARIATION.— MALE (n=2): total length: 6.0–6.09. Carapace length: 2.4–2.56. Abdomen length: 3.53–3.60. Femur I length: 1.90–1.92. Tibia I length: 1.52–1.64. Patella length: 0.96–1.10.

FEMALE: Unknown.

NATURAL HISTORY.— Specimens were collected from mixed tropical forest by pitfall traps and by beating low vegetation.

DISTRIBUTION.— Central southern Madagascar.

***Padilla cornuta* (Peckham and Peckham, 1885)**
Figures 5, 8A, 13A, 25C, 29A–C, 45–46, 62A–B.

Icius cornutus Peckham and Peckham, 1885a:30–32 (syntype male and female from Madagascar, MCZ type 115, examined). *Padilla cornuta* Peckham and Peckham, 1894:130. Prószyński, 1987:74. Platnick 2006.

MATERIAL EXAMINED.— MADAGASCAR: **Antananarivo Province:** Andranomay, 11.5 km 147° SSE Anjozorobe, 1300 m, 18°28′24″S, 47°57′36″E, 5–13 December 2000, Fisher/Griswold Arthropod team 2♂ (CAS), CASENT9004193 – 2♀ 11 juveniles (CAS), CASENT9021863 – 3♀ 8 juveniles (CAS), CASENT 9003868. Reserve speciale d'Ambohitantely, 20.9 km 72° NE Ankazobe, 1410 m, 18°13′31″S, 47°17′13″E, 17–22 April 2001, Fisher/Griswold Arthropod team, 2♀ (CAS), CASENT 9021861 – 1♂ (CAS), CASENT 9001225. **Toamasina Province**: Montagne d'Anjanaharibe 19.5 km NNE of Ambinanitelo, 1100 m, 15.178333°S, 49.635°E, 12–16 March 2003, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9020140.

Fianarantsoa Province: Park National Ranomafana, 900m, 21°15′S, 47°25′E, 5–7 December 1993, C. Griswold, 1♂ (CAS), CASENT 9020186.

DIAGNOSIS OF THE *CORNUTA* GROUP.— Distinguished from other male *Padilla* not included within the *Cornuta* group by having: (1) a pair of horns projecting forward from the proximal parts of the chelicerae, dorsally straight and converging near the tips, but neither touching nor crossing each other, laterally presenting a double curve (Figs. 3A–B) (2) tegulum division of the palp is a shallow invagination, except in *P. cornuta* (Figs. 29E–H).

DIAGNOSIS OF *P.CORNUTA*.— Different from other males within the *cornuta* group by the following combinations of characters (1) horns are cylindrical with dark sharp edges and often with pigmentation at their bases, strong and thicker, going upwards till the apex (Figs. 13A), (2) carapace with a white guanine deposit that is constricted by two black spots at its median part (different from *P. manjelatra* and *P. lavatandroka*) (Fig. 8A), (3) tibia with a median proximal spur (Fig. 25C) and (4) abdomen is yellowish with two thick dark lateral bands (Figs. 5, 8A).

Palp with a protuberance (pb) on anterior retrolateral side (Figs. 29A–C), and the basal prolateral of which is divided by a horizontal slit (only on the basal prolateral side in all other male *Cornuta* group; Figs. 29E–H). Tegular division of the palp forming a large longitudinal hole as in the *Armata* group species (Fig. 29B). Retrolateral tibial apophysis relatively long (extending till the mid-length of the cymbium), slightly converging to the cymbium. Velum is absent (Figs. 29A–C).

DESCRIPTION.— MALE (from Ankazobe, Ambohitantely, Antananarivo, Madagascar): Carapace and abdomen are dark on lateral sides; a thick yellowish band is present on the median part of the cephalothorax and abdominal dorsum. The abdomen has also one pair of dark patches (Fig. 5).

Total length: 5.92. Carapace length: 2.56. Abdomen length: 3.36. Horn length/carapace length: 0.50. Horn width: 0.22. DH: 0.52. DH/CHL: 0.81. Width ocular field I: 1.43. Width ocular field III: 1.43. Height cephalothorax: 0.80. Diameter AME/length chelicerae: 0.78. Height cephalothorax/width cephalothorax: 0.42. Width cephalothorax/width ocular field III: 1.32.

Femur I/width ocular field III: 1.38. Femur III/width ocular field III: 0.75. Femur IV/Femur III: 1.20. Tibia I/ width ocular field III: 1.09. Tarsi I/ metatarsi I: 0.52.

Promargins of chelicerae are pluridentate with five teeth continued with a sharp line; retromargins are fissidentate with five points.

VARIATION.— MALE (n=3): total length: 4.36–5.92. Carapace length: 1.96–2.56. Abdomen length: 2.4–3.36. Femur I length: 1.06–1.98. Horn length/carapace length: 0.43–0.60. Horn width: 0.14–0.22.

NOTE.— Males of *Padilla cornuta* exhibit a case of allometry. Larger males have stronger body and horns and dark ventral abdomens, whereas smaller ones are very weak looking and with whitish ventral abdomens. The distribution of those two variants overlapped in the central part of the island.

FEMALE (from, Ankazobe, Ambohitantely, Antananarivo, Madagascar): As male, except that dorsal abdomen provided with one to two pairs of dark yellowish patches (male patches are not very distinct). Ventral abdomen is yellowish with dark round spots around the spinnerets: one dark purple above, and one or two pairs on lateral sides. Also, cervical groove is more obvious in females than in the male.

Total length: 5.49. Carapace length: 2.53. Abdomen length: 2.96. Cephalothorax widths: 1.63. Width ocular field I: 1.40. Width ocular field III: 1.40. Height cephalothorax: 0.70.

Femur I/ width ocular field III: 1.01. Femur III/ width ocular field III: 0.66. Tibia I/ width ocular field III: 0.71. Tibia III/ tibia IV: 0.66. Patella III/ tibia III: 1.08.

Promargins of the chelicerae are pluridentate with three teeth continued with a sharp line; retromargins are fissidentate with five points.

Genitalia with the copulatory openings (co) not interconnected but rather widely separated at their anterior parts. The fertilization ducts (fd) and the spermathecae (spc) form a large coil at the posterior parts of the epigynum (Figs. 62A–B.).

VARIATION.— FEMALE (n=5): total length: 4.31–5.99. Carapace length: 1.96–2.53. Abdomen length: 2.35–3.66. Cephalothorax width: 1.23–1.63. Femur I length: 1.06–1.42. Patella III/ tibia III: 1–1.083.

NATURAL HISTORY.— Specimens were collected from mountain forest, mixed tropical rainforest by general collecting, and by beating low vegetation.

DISTRIBUTION.— Central, central southern, eastern, and central western parts of Madagascar (Figs. 45, 46).

***Padilla manjelatra* Andriamalala, sp. nov.**

Figures 3A, 6, 8B, 13C, 24D, 25B, 29D–F, 62C–D.

MATERIAL EXAMINED.— MALE HOLOTYPE AND FEMALE PARATYPE: MADAGASCAR: **Antsiranana Province**: Marojejy reserve, 8.4 km NNW of Manantenina, 700m, 14°26′S, 49°45′E, 10–16 November 1993, mountain rainforest, general collecting and beating low vegetation, C. Griswold, J. Coddington, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ 1♀ (CAS), CASENT9021900. OTHER MATERIAL EXAMINED: MADAGASCAR: **Antsiranana Province:** Reserve Speciale de Manongarivo, 12.8 km 228° SW of Antanambao, 780 m, 13°58.6′S, 48°25.4′E, 12 October 1992, 1♂ (CAS), CASENT9021862. Binara forest, 9.4 km 235° SW Daraina, 1100m, 13°14.5′48″S, 49°36′E, 6 December 2003, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT 9011917.

ETYMOLOGY.— The species name is from the Malagasy word "manjelatra," which means "brilliant".

DIAGNOSIS.— Distinguished from *P. cornuta* by the following characters: (1) horns very long, almost as long as the carapace (horn length/carapace length: 0.8), thicker (horn width: 0.34), slightly outward at the base, then converging, upturned or touching each other at tips, horns not flattened dorso-ventrally but cylindrical and without a pigment deposit at their bases as in *P. cornuta* (Figs. 3A–B), (2) presence of spur both on tibia I and patella I (Fig. 25B), (3) carapace higher and greatly enlarged between legs II and III, without a white guanine deposit as in *P. cornuta* (Figs. 3A–B), (4) endites have ridges that extend to their bases (same as in Fig. 30D) and (5) palp without a protuberance on the anterior retrolateral side (different from *P. cornuta*) (Figs. 29D-E-F). Body dark, high (CH/CL >0.35), compact and robust compared with *P. cornuta* (Figs. 6, 8B). Legs light orange.

DESCRIPTION.— MALE (Holotype from Marojejy, Antsiranana, Madagascar): Carapace and abdomen completely black with horizontal stripes of green iridescent hairs. Those horizontal stripes of scale-like hairs become lighter at the posterior part of the abdomen. All eyes are surrounded with black pigmentation. All legs are yellowish to orange. Tibia and metatarsi of the first legs are black (Figs. 6, 24D).

Total length: 5.72. Carapace length: 2.86. Abdomen length: 2.86. Horn length/carapace length: 0.80. Horn width: 0.34. DH: 0.56. DH/CHL: 0.8. Width ocular field I: 1.93. Width ocular field III: 1.86. Height cephalothorax: 1.16. Diameter AME/length chelicerae: 0.98. Height cephalothorax/width cephalothorax: 0.49. Width cephalothorax/width ocular field III: 1.27.

Femur I/width ocular field III: 1.27. Femur III/width ocular field III: 0.78. Femur IV/Femur III: 1.14. Tibia I/width ocular field III: 0.87. Tarsi I/metatarsi I: 0.56.

Promargins of the chelicerae are pluridentate with three teeth; retromargins are fissidentate with four points.

Retrolateral tibial apophysis is short with rounded tip, curved toward the cymbium.

VARIATION.— MALE (n=3): total length: 5.19–6.53. Carapace length: 2.56–3.03. Abdomen

length: 2.63–3.50. Femur I length: 2.04–3.05. Horn length/carapace length: 0.71–0.80. Horn width: 0.20–0.34.

FEMALE (Paratype from Marojejy, Antsiranana, Madagascar): As male but legs darker with black stripe.

Total length: 5.76. Carapace length: 2.50. Abdomen length: 3.26. Cephalothorax width: 2.06. Width ocular field I: 1.83. Width ocular field III: 1.76. Height cephalothorax: 1.0.

Femur I/ width ocular field III: 0.97. Femur III/ width ocular field III: 0.71. Tibia I/ width ocular field III: 0.70. Tibia III/ tibia IV: 0.76. Patella III/ tibia III: 1.03.

Promargins of the chelicerae are pluridentate with four distal teeth followed by a proximal sharp line; retromargins are fissidentate with four points.

Genitalia sclerotized with the copulatory openings interconnected at the anterior parts of the epigynum (different from *P. cornuta*, Figs. 62C–D).

NATURAL HISTORY.— Specimens were collected from rainforest and mountain forest by general collecting and beating low vegetation.

DISTRIBUTION.— Northern Madagascar.

***Padilla lavatandroka* Andriamalala, sp. nov.**

Figures 2A–C, 4A–a, 7, 8C, 13B, 14B, 28A, 29G–I, 30A–D, 52A, 52D–E, 53B–D, 54A–F, 56A–F, 62E–F.

MATERIAL EXAMINED.— MALE HOLOTYPE AND FEMALE PARATYPE: MADAGASCAR: **Antsiranana Province:** National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000 m, 12°32′S, 49°10′E, 21–30 November 1993, mountain rainforest, beating low vegetation, C. Griswold, J. Coddington, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ 1♀ (CAS), CASENT9020190. OTHER MATERIAL EXAMINED: MADAGASCAR: **Antsiranana Province:** National Parc Montagne d'Ambre, 12.2 km 211° SSW of Joffreville, 1300m, 12°35′47″S, 49°9′34″E, 2–7 February 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9006890. National Parc Montagne d'Ambre, 12.2 km 211° SSW of Joffreville, 1000–1200 m, 12°31′53.5″S, 49°10′36.8″E, 14–20 December 2005, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9023436. National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000m, 12° 32′S, 49° 10′E, 21–30 June 1993, C. Griswold, J. Coddington, N. Scharff, S. Larcher and R. Andriamasimanana, 5♂ 3♀ 1juvenile (CAS). CASENT9021901 – 3♂ 2♀ (CAS), CASENT9020190 – 3♂ 4♀ (CAS), CASENT-9020189. National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000 m, 12°32′S, 49°10′E, 21–30 November 1993, C. Griswold, J. Coddington, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ 2♀ (CAS), CASENT 9025471.

ETYMOLOGY.— The species name is from the Malagasy words "lava tandroka," which means "with long horns."

DIAGNOSIS.— Body, carapace and horns are the same as *P. manjelatra*, but distinguished from it by the following characters: (1) tibia I without a spur (Figs. 7, 8C), (2) abdomen with a dark brown scutum (sclerotized plate) and yellow reticulations instead of *transverse* stripes of iridescent green scale-like hairs, body and legs rather brown, (3) palp is very simple, without any protuberance (same as in *P. manjelatra*, but different from *P. cornuta*) (Figs. 29G–I) and (4) embolus tip is different from all other *Padilla* by being circular.

DESCRIPTION.— MALE (Holotype from National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, Antsiranana, Madagascar): Carapace, abdomen and legs dark brown. Male may have few iridescent green scales on the abdomen. All legs brownish orange. First legs dark yellow with the tibia and metatarsi darkened as in *P. manjelatra*. The other legs yellowish with horizontal brown chocolate stripes (Fig. 7).

Total length: 6.63. Carapace length: 3.10. Abdomen length: 3.51. Horn length/carapace length: 0.79. Horn width: 0.32. DH: 0.80. DH/CHL: 0.87. Width ocular field I: 1.96. Width ocular field III:

1.80. Height cephalothorax: 1.33. Diameter AME/length chelicerae: 0.69. Height cephalothorax/width cephalothorax: 0.52. Width cephalothorax/width ocular field III: 1.42.

Femur I/width ocular field III: 1.50. Femur III/width ocular field III: 0.90. Femur IV/Femur III: 1.09. Tibia I/width ocular field III: 1.04. Tarsi I/metatarsi I: 0.50.

Promargins of chelicerae pluridentate with four teeth, retromargins fissidentate with five points.

Palp tegular division not a groove, but rather a shallow longitudinal invagination. Posterior part of the tegulum not visible from the ventral side. Velum absent. Retrolateral tibial apophysis short, straight with a round tip (Fig. 29G-H-I).

Variation.— Male (n=5): total length: 5.13–6.63. Carapace length: 2.50–3.10. Abdomen length: 2.63–3.53. Femur I length: 1.88–2.70. Horn length/carapace length: 0.75–0.81. Horn width: 0.28–0.32.

Female (Paratype from National Parc Montagne d'Ambre, 2.79 air km NE of Parc entrance, Antsiranana, Madagascar): Carapace brown orange with lines of brilliant white hairs on lateral sides between eyes and edges, slightly longer than wide. Dorsum brown chocolate with yellowish reticulations; bears two pairs of dark patches. Legs as in male but tibia and metatarsi of leg I not darkened.

Total length: 6.42. Carapace length: 3.16. Abdomen length: 3.26. Cephalothorax width: 2.50. Width ocular field I: 2.06. Width ocular field III: 1.96. Height cephalothorax: 1.26.

Femur I/width ocular field III: 1.08. Femur III/width ocular field III: 0.83. Tibia I/width ocular field III: 0.81. Tibia III/tibia IV: 0.73. Patella III/tibia III: 1.09.

Promargins of the chelicerae pluridentate with four distal teeth and a proximal sharp line, retromargins fissidentate with five points.

Genitalia: distinguished from *P. manjelatra* by having the copulatory openings (co) not interconnected at their anterior part (Figs. 62E–F).

Variation.— Female (n=5): Total length: 6.42–6.93. Carapace length: 3.06–3.33. Abdomen length: 3.26–3.73. Cephalothorax width: 2.43–2.63. Femur I length: 2.10–2.38. Patella III/tibia III: 1.07–1.16.

Natural history.— Specimens were collected from mountain forest by beating low vegetation.

Distribution.— Northern Madagascar.

Padilla mitohy Andriamalala, sp. nov.

Figures 27A, 27 C–E, 34A–E.

Material examined.— Holotype: Madagascar: **Antsiranana Province:** Reserve Naturelle Integrale de Lokobe, 6.3 km ESE of Hellville, 30 m, 13°25′10″S, 48°19′52″E, 19–24 March 2001, rainforest, general collecting and beating low vegetation, Fisher/Griswold Arthropod survey team, 1♀ (CAS), CASENT 9007991. Other material examined: Madagascar: **Antsiranana Province**: Nosy Be, Reserve Naturelle Integrale de Lokobe, 6.3 km 112° ESE Hellville, 30 m, 13°25′10″S, 48° 19′52″E, 19–24 March 2001, Fisher/Griswold Arthropod team 1♀ (CAS), CASENT9007991 – 1♀ (CAS), CASENT9007992 – 1♀ (CAS), CASENT9003237 – 1♀ (CAS), CASENT9025473. Forêt d'Andavakoera, 21.4 km 75° ENE Ambilobe; 4.6 km 356° N Betsiaka, 425m, 13°07′06″S, 49°13′48″E, 15 December 2003, Fisher/Griswold Arthropod team, 2♀ (CAS), CASENT 9011933. Reserve Special de l'Ankarana, 13.6 km 192° SSW Anivorano Nord, 210 m, 12°51′49″S, 49°13′33″E, 16–20 February 2001, Fisher/Griswold Arthropod team, 3 ♀ (CAS), CASENT 9001478.

Etymology.— The species name is from the Malagasy word "*mitohy*" meaning "continuous."

Diagnosis.— Distinguished from females of *P. manjelatra* and *P. lavatandroka* by the follow-

ing characters: (1) body elongate and not globular (Fig. 34A), (2) carapace shorter than the abdomen, with longitudinal bands of white scales on the lateral sides, (3) abdomen dark brown with a dorsal folium instead of reticulations, (4) tibia of first legs enlarged compared with other leg segments and provided with thick fringe of setae and (5) epigynum anterior part not fully sclerotized (only the part around the two copulatory pockets is sclerotized), copulatory openings not interconnected and continued posteriorly with the sclerotized tube or "sulci" as in *P. foty* (Figs. 27C–E, 34E).

Description.— Female (Holotype from Réserve Naturelle Integrale de Lokobe, 6.3 km ESE of Hellville, Antsiranana, Madagascar): Carapace dark brown with lateral thick lines of white scales. Abdomen dark with a median folium and yellowish lateral sides. First legs dark brown except tarsi which are yellow. All the other legs yellow. Metatarsi provided with one dark ventral spot that extended beyond the two metatarsal spines (Figs. 27A, 34A).

Total length: 5.92. Carapace length: 2.16. Abdomen length: 3.76. Cephalothorax width: 1.50. Width ocular field I: 1.16. Width ocular field III: 1.23. Height cephalothorax: 0.63.

Femur I/width ocular field III: 0.96. Femur III/width ocular field III: 0.66. Tibia I/width ocular field III: 0.85. Tibia III/tibia IV: 0.57. Patella III/tibia III: 1.11.

Promargins of the chelicerae pluridentate with two distal teeth and a sharp line. Retromargins pluridentate with six distal small teeth.

Genitalia: Epigynum having the copulatory openings not interconnected, and followed posteriorly by lateral sulci (tube connecting the copulatory openings to the posterior part of the epigynum). Spermathecae narrower.

Variation.— Female (n=5): total length: 5.26–5.92. Carapace length: 2.03–2.16. Abdomen length: 3.1–3.76. Cephalothorax width: 1.36–1.53. Femur I length: 1.18–1.44. Patella III/tibia III: 1.10–1.15.

Male.— Unknown.

Natural history.— Specimens were collected from rainforest by beating low vegetation.

Distribution.— Northern Madagascar.

***Padilla mihaingo* Andriamalala, sp. nov.**

Figures 27B–F, 34B–F.

Material examined.— Holotype: Madagascar: **Antsiranana Province:** Forêt d'Ampondrabe, 26.3 km NNE of Daraina, 175 m, 12°58′12″S, 49°42′E, 10 December 2003, tropical dry forest, general collecting by day Fisher/Griswold Arthropod survey team, 1 ♀ (CAS), CASENT9011958.

Etymology.— The species name is from the Malagasy word "mihaingo," which means "dressed up."

Diagnosis.— Distinguished from other females like *P. mitohy* by the following characters: (1) copulatory openings interconnected at the anterior part of the epigynum and not followed by lateral sulci, spermathecae are broader (Figs. 27D–F), (2) femur III dorsal without an additional promarginal distal spine like in *P. mitohy* and (3) width ocular field III narrower than width ocular field I (contrary to *P. mitohy*).

Description.— Female (Holotype from Forêt d'Ampondrabe, 26.3 km NNE of Daraina, Antsiranana, Madagascar): Coloration same as *P. mitohy* (Figs. 27B, 34B).

Total length: 5.52. Carapace length: 2.16. Abdomen length: 3.36. Cephalothorax width: 1.50. Width ocular field I: 1.16. Width ocular field III: 0.70. Height cephalothorax: 0.70.

Femur I/width ocular field III: 1.74. Femur III/width ocular field III: 1.22. Tibia I/width ocular field III: 1.51. Tibia III/tibia IV: 0.57. Patella III/tibia III: 0.91.

Promargins of chelicerae pluridentate with three distal teeth and a proximal sharp line; retromargins fissidentate with six points.

MALE.: Unknown.

NATURAL HISTORY.— Specimen was collected from tropical dry forest by general collecting by day.

DISTRIBUTION.— Northern Madagascar.

***Padilla foty* Andriamalala, sp. nov.**

Figures 34C–G.

MATERIAL EXAMINED.— HOLOTYPE: MADAGASCAR: **Antsiranana Province**: Reserve Integralle Naturelle de Lokobe, 6.3 km ESE of Hellville, 30 m, 13°25′10″S, 48°19′52″E, 19–24 March 2001, rainforest, beating low vegetation, J.J. Rafanomezantsoa et al., 1 ♀ (CAS), CASENT 9021859.

ETYMOLOGY.— The species name is from the Malagasy word "*foty,*" which means "white."

DIAGNOSIS.— Distinguished from *P. mitohy* and *P. mihaingo* by the following characters: (1) carapace without bands of white scales on lateral sides, (2) abdominal dorsum yellowish with thin lateral dark bands instead of a folium (Fig. 34C), (3) spinnerets not preceded with a plate, (4) copulatory openings not interconnected, spermathecae narrower, and sulci present (different from *P. mihaingo)* (Fig. 34G) and (5) femur III dorsal with an additional pro-marginal distal spine as *P. mihaingo*.

DESCRIPTION.— FEMALE (Holotype from Reserve Integralle Naturelle de Lokobe, 6.3 km ESE of Hellville, Antsiranana, Madagascar): Carapace yellowish white with brown lines on lateral sides. Abdomen dorsum whitish with two dark median lateral bands terminated by horizontal spots at posterior part, venter uniformly whitish. Spinnerets not preceded by a plate (Fig. 34G).

Total length: 4.96. Carapace length: 2.06. Abdomen length: 2.90. Cephalothorax width: 1.46. Width ocular field I: 1.20. Width ocular field III: 1.20. Height cephalothorax: 0.56.

Femur I/width ocular field III: 1.13. Femur III/width ocular field III: 0.73. Tibia I/width ocular field III: 0.88. Tibia III/tibia IV: 0.60. Patella III/tibia III: 0.92.

Retromargins of chelicerae pluridentate with five teeth, promargins pluridentate with three distal teeth and a proximal sharp line

MALE: Unknown.

NATURAL HISTORY.— The type specimen was collected from tropical rainforest by beating low vegetation.

DISTRIBUTION.— Northern Madagascar.

***Padilla boritandroka* Andriamalala, sp. nov.**

Figures 3G–H, 4A–b, 11A, 14E, 17A, 24B, 28D, 32A-B-C, 55.

MATERIAL EXAMINED.— HOLOTYPE: MADAGASCAR: **Antsiranana Province:** Reserve speciale Manongarivo, 10.8 km SW of Antanambao, 400 m, 13°57.7′S, 48°26′E, 8 November 1998, tropical rainforest, beating low vegetation, B.L. Fisher, 1 ♂ (CAS), CASENT 9020178. OTHER MATERIAL EXAMINED: MADAGASCAR: **Antsiranana Province:** Forêt d' Antsahabe, 11.4 km 275° W Daraina, 550m, 13°12′42″S, 49°33′24″E, 12 December 2003, Fisher/Griswold Arthropod team, 1 ♂ (CAS), CASENT9011931. Reserve special d'Ambre, 3.5 km 275° SW Sakaramy, 325 m, 12°28′8″S, 49°14′32″E, 26–31 January 2001, Fisher/Griswold Arthropod team, 1 ♂ (CAS), CASENT 9006821. Reserve special d'Ambre, 3.5 km 275° SW Sakaramy, 325 m, 12°28′8″S, 49°14′32″E, 26–31 January 2001, Fisher/Griswold Arthropod team, 1 ♂ (CAS), CASENT 9004544. Reserve special Manongarivo, 10.8 km 229° SW of Antanambao, 780 m, 13°57.7′S, 48°26.0′E, 12 October 1998, Fisher/Griswold Arthropod team, 1 ♂ (CAS), CASENT9020177. **Mahajanga Province:** Parc National Baie de Baly, 12.4 km 337° NNW of Soalala, 10 m, 16°0′36″S, 45°15′54″E, 26–30 June 2002, Fisher/Griswold

Arthropod team, 1♂ (CAS), CASENT3006885. Parc National Tsingy de Bemaraha, 10.6 km 123° ESE of Antsalova, 150 m, 19°42′34″S, 44°43′5″E, 16–20 June 2001, Fisher/Griswold Arthropod team, 1♂ (CAS), CASENT9009733.

Etymology.— The species name is from the Malagasy words "bory tandroka," which means "with short horns."

Diagnosis of the *Brevis* group.— Species within the *Brevis* group are distinguished from other male *Padilla* by having: (1) short horns that originate from the distal part of the chelicerae and which are straight (Figs. 3G–H, 14D–E), (2) chelicerae projecting forward and parallel to the carapace instead of perpendicular to it (Figs. 3G–H, 4A–b) and (3) paturons flattened dorsally with promarginal and retromarginal sharpened edges (Figs. 14D–E).

Diagnosis of *P. boritandroka*.— Male *P. boritandroka* are distinguished from male *P. ngeroka* by the following characters: (1) horns extremely short (horn length/carapace length: 0.02), more or less thick (horn width/horn length: 0.66), converging to each other, with the tips slightly oriented outward, horns arise from the apex of the chelicerae, near the fangs (Fig. 3G), (2) tibia of the first legs extremely fat and provided with a thick promarginal tuft of black hairs (tibia slightly wider than femur and bearing a proventral sparse fringe of black hairs in *P. ngeroka*), (3) patella and femur retrodistally with thick tuft of hairs and (4) promarginal teeth not very large as in *P. ngeroka*.

Description.— Male (Holotype from Réserve spéciale Manongarivo, 10.8 km SW of Antanambao, Antsiranana, Madagascar): Carapace dark or brown, sometimes with spots of white scales on lateral posterior margins. Top of the carapace brown yellowish, flattened, with two black spots. Abdomen dorsum generally brown to brown yellowish, with one median dark band followed laterally by two other dark lateral stripes. In some specimens the dorsum is covered with a dark scutum (sclerotized plate). Also, one pair of whitish spots or a tuft of white scales are sometimes observed on the anteromedian of the dorsum. First legs greatly enlarged and completely dark brown to black, except tarsi which are whitish. All the other legs whitish with lateral maculae (dark lateral patches) on femora and tarsi. Patella and tibia both with retroventral fringe of black hairs (Fig. 55). Top of the carapace and the abdomen are both flattened. Chelicerae longer than wide, dorsoventrally flattened, with sharpened lateral edges and bases widely separated from each other. Fangs long (14E).

Total length: 5.22. Carapace length: 2.16. Abdomen length: 3.06. Horn length/carapace length: 0.02. Horn width: 0.04. DH: 0.12. DH/CHL: 0.23. Width ocular field I: 1.20. Width ocular field III: 1.16. Height cephalothorax: 1.56. Diameter AME/length chelicerae: 0.95. Height cephalothorax/width cephalothorax: 0.52. Width cephalothorax/width ocular field III: 1.34.

Femur I/width ocular field III: 1.44. Femur III/width ocular field III: 0.70. Femur IV/Femur III: 1.29. Tibia I/width ocular field III: 1.27. Tarsi I/metatarsi I: 0.44.

Variation.— Male (n=5): total length: 4.66–5.22. Carapace length: 1.63–2.16. Abdomen length: 2.23–3.06. Diameter AME: 0.31–0.45. Femur I length: 1.16–1.68. Horn length/carapace length: 0.02–0.08. Horn width: 0.03–0.08.

Female: Unknown.

Natural history.— Specimens were collected from tropical dry forest and tropical rainforest by beating low vegetation and general collecting by day.

Distribution.— Western and northern Madagascar.

***Padilla ngeroka* Andriamalala, sp. nov.**

Figures 3H, 4A–B, 11B, 14D, 17B, 32D–F, 34H, 45–46, 63.

Material examined.— Male holotype and female paratype: Madagascar: **Antananarivo**

Province: Andranomay, 11.5 km SSE of Anjozorobe, 1300 m, 18°28′24″S, 47°57′36″E, 5–13 December 2000, mountain rainforest, general collecting, Fisher/Griswold Arthropod survey team, 1♂ 1♀ (CAS), CASENT9004188. OTHER MATERIAL EXAMINED: MADAGASCAR: **Antananarivo Province**: Andranomay, 11.5 km SSE of Anjozorobe, 1300 m, 18°28′S, 47°57′36″E, 5–13 December 2000, Fisher/Griswold Arthropod Survey team, 1♂ (CAS), CASENT9025472. National Park Montagne d'Ambre, 2.79 air km NE of Parc entrance, 1000m, 12°32′S, 49°10′E, 21–30 November 1993, C. Griswold, N. Scharff, J. Coddington, S. Larcher, and R. Andriamasimanana, 5♂ 3♀ 1 juvenile (CAS), CASENT9021901 – 3♂ 2♀ (CAS), CASENT9020190 – 3♂ 4♀ (CAS), CASENT9020189. **Fianarantsoa Province**: National Park Ranomafana, N.P Maharira, below summit herb layer, 8 April 1992, S. Kariko and V. Roth, 1♂ MCZ, MCZ65435. National Park Ranomafana, 2.3 km N of Vohiparara village, 18 April 1998, C. Griswold, D. Kavanaugh, N. Penny, M. Raherilalao, E. Rajeriarison, J. Ranorianarisoa, J. Schweikert, and D. Ubick, 1♀ (CAS), CASENT9021864. National Park Ranomafana, Talatakely, 900 m, 21°15′S, 47°25′E, 5–7 July 1993, C. Griswold, N. Scharff, S. Larcher, and R. Andriamasimanana, 1♂ (CAS), CASENT 9020187.

ETYMOLOGY.— The species name is from the Malagasy expression "mainty ngeroka," which means completely dark or black.

DIAGNOSIS.— Distinguished from male *P. boritandroka* by having (1) the horns cylindrical, directed downwards and slightly longer, as long as one third of the carapace (horn length/carapace length: 0.26) (Figs. 3H, 4A–b, 14D), the horns arise from the distal part of the paturon, just above the fangs (slightly higher compared to *P. boritandroka,* Fig. 3H), (2) serrula not extending to the bases of endites, (3) tibiae of first legs are slightly wider than the femur and bear a sparse retroventral fringe of black hairs (tibiae are greatly enlarged and with a thick tuft of hairs in *P. boritandroka*) likewise femur I retrodistal and patella with sparse hairs (not with thick fringe as in *P. boritandroka)* and (4) promargins of the chelicerae pluridentate with four enormous teeth.

DESCRIPTION.— MALE (Holotype from Andranomay, 11.5 km SSE of Anjozorobe, Antananarivo, Madagascar): Both carapace and abdomen dark brown and flattened. Abdomen sometimes provided with dark sclerotized scutum. First legs completely dark except tarsi, the other legs yellowish (Fig. 63).

Total length: 4.75. Carapace length: 2.02. Abdomen length: 2.73. Horn length/carapace length: 0.26. Horn width: 0.1. DH: 0.12. DH/CHL: 0.26. Width ocular field I: 1.05. Width ocular field III: 1.10. Height cephalothorax: 0.57. Diameter AME/length chelicerae: 0.87.

Femur I/width ocular field III: 1.33. Femur III/width ocular field III: 0.60. Femur IV/Femur III: 1.36. Tibia I/width ocular field III: 1.09. Tarsi I/metatarsi I: 0.38. Height cephalothorax/width cephalothorax: 0.42. Width cephalothorax/width ocular field III: 1.21.

Dentition same as *P. boritandroka,* but promarginal teeth very large.

VARIATION.— MALE (n=3): total length: 4.63–5.06. Carapace length: 1.93–2.06. Abdomen length: 2.70–3. Femur I length: 1.44–1.52. Horn length/carapace length: 0.19–0.26. Horn width: 0.08–0.1.

FEMALE (Paratype from Andranomay, 11.5 km SSE of Anjozorobe, Antananarivo, Madagascar)**:** Females are quite different from males. Both carapace and abdomen yellowish with dark lateral bands that are interrupted at their posterior parts (different from other female *Padilla*). Carapace flattened on its top and with a white guanine deposit on the anterior region. Female abdomen not flattened, and longer and broader.

Total length: 4.46. Carapace length: 1.73. Abdomen length: 2.73. Cephalothorax width: 1.71. Width ocular field I: 0.95. Width ocular field III: 0.95. Height cephalothorax: 0.46.
Femur I/width ocular field III: 0.76. Femur III/width ocular field III: 0.589. Tibia I/width ocular field III: 0.57. Tibia III/tibia IV: 0.63. Patella III/tibia III: 0.96.

Promargins of chelicerae pluridentate with four teeth and a proximal sharp line, retromargins pluridentate with six teeth.

Genitalia: copulatory openings not interconnected at their anterior part. Septum present. On the posterolateral part, the fertilization ducts are straight, short, parallel, and continued with two small spermathecae (that are close to each other, Fig. 34H).

Variation.— Female (n=5): total length: 6.42–6.93. Carapace length: 3.06–3.33. Abdomen length: 3.26–3.73. Cephalothorax width: 2.43–2.63. Femur I length: 2.10–2.38. Patella III/tibia III: 1.073–1.162.

Natural history.— Specimens were collected from mountain forest by beating low vegetation.

Distribution.— Northern Madagascar (Figs. 45–46).

Nomina dubia

Padilla glauca Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species.

Padilla lancearia Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species.

Padilla mantis Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species.

Excluded species

Padilla javana Simon, 1900: The type could not be located at the Muséum National d'Histoire Naturelle de Paris, and Simon's (1900) description does not provide sufficient detail to recognize this species. Fortunately, Prószyński (2003) has examined other specimens of this southeast Asian species. *Padilla javana* lacks the extraordinary embellishments (horns) that are synapomorphic for all male *Padilla* (Prószyński, 2003), and therefore this species, from Java, is excluded from *Padilla*.

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Illustrations (Figures 2–63) and Appendicies 1–4

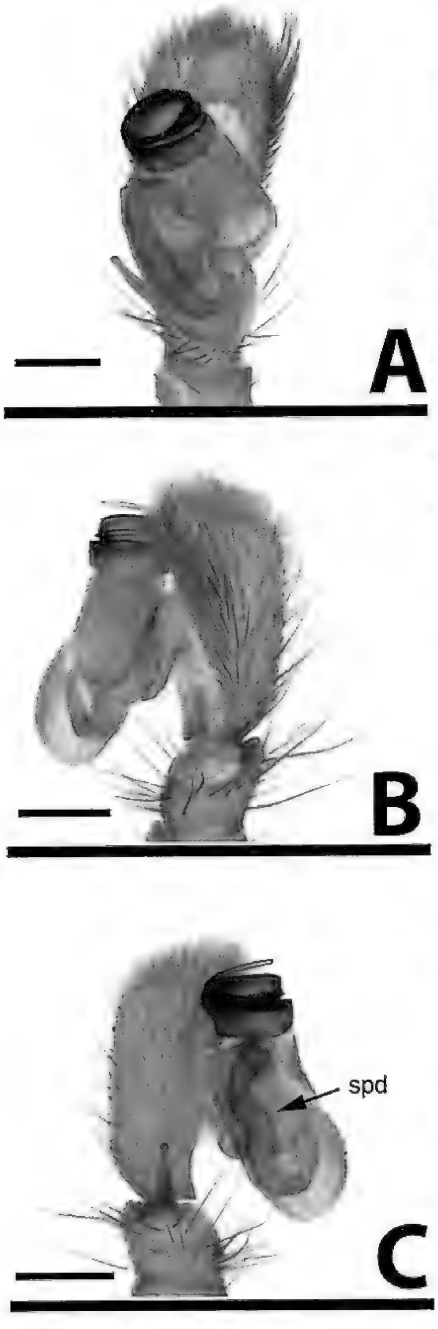


FIGURE 2. *Padilla lavatandroka*, expanded right palp. A. palp, ventral. B. palp, prolateral. C. palp, retrolateral. Scale bars for all = 0.2 mm.

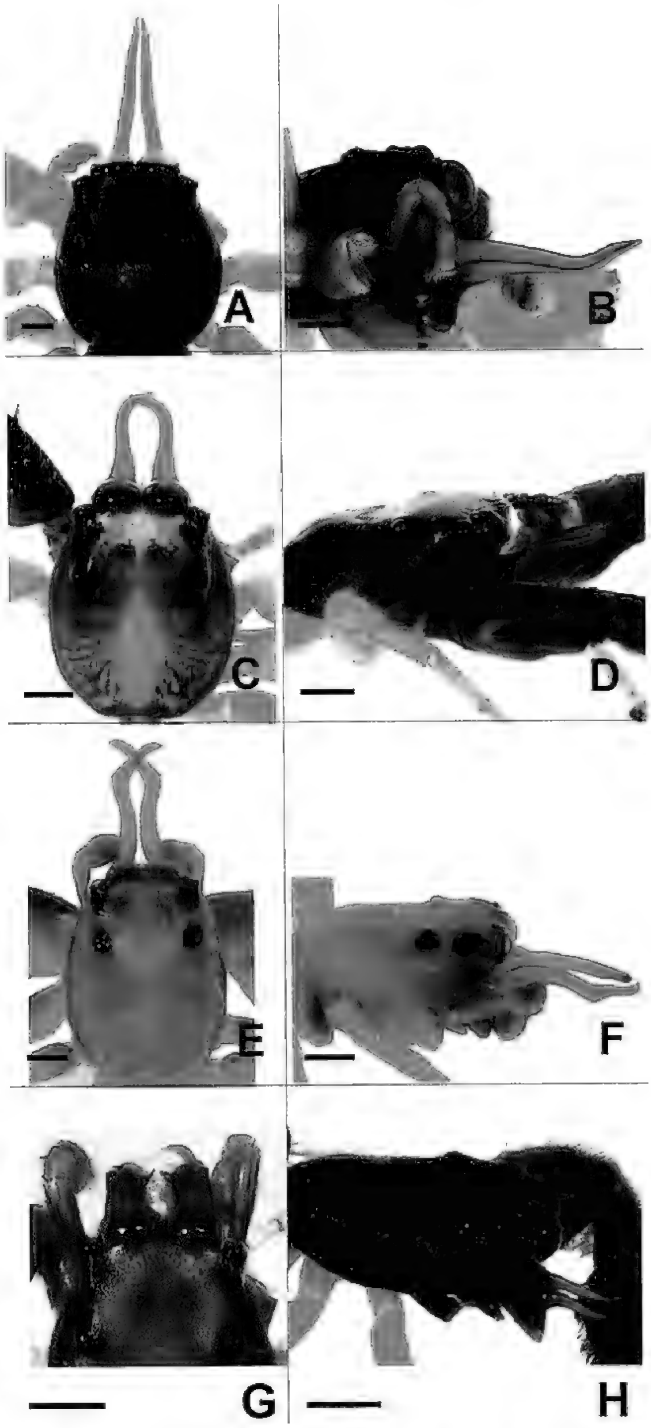


FIGURE 3. Male horn orientation dorsal and lateral view. A. *P. manjelatra*, carapace, dorsal. B. carapace, lateral. C. *P. mazavaloha*, carapace, dorsal. D. carapace, lateral. E. *P. armata* carapace, dorsal. F. carapace lateral. G. *P. boritandroaka* carapace, dorsal. H. *P. ngeroka* carapace, lateral. Scale bars for A, B, C, D, E, F = 0.5 mm.

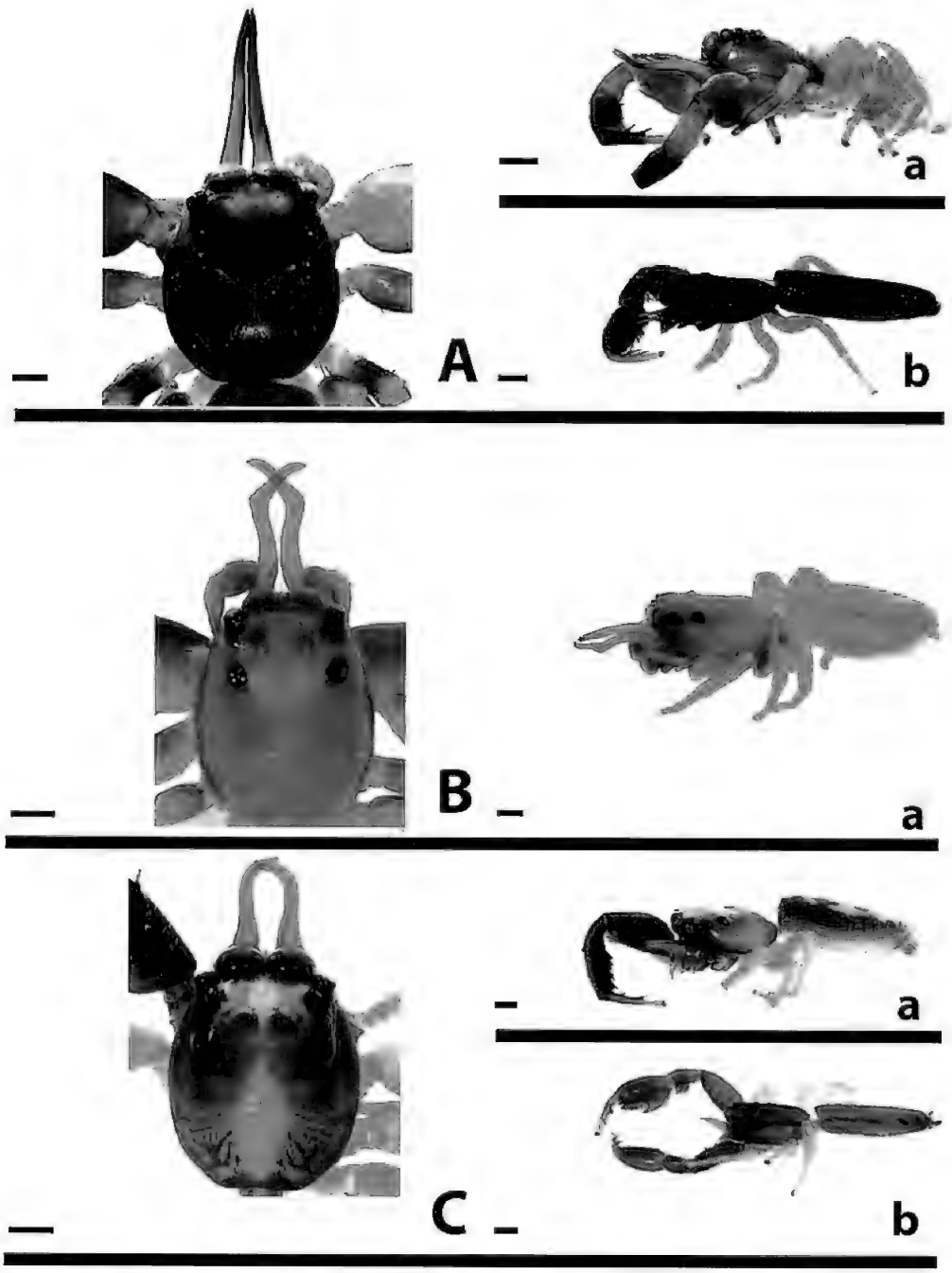


FIGURE 4. *Padilla* horn orientation, body shape. A. *P. lavatandroka*, horn, dorsal, straight. a. laterally is showing a double curve with tips upward; body protruding. b. *P. boritandroka*, laterally going downward; body flattened. B. *P. armata*, horn, dorsal, having a double curve. a. laterally going downward; body intermediate. C. *P. mazavaloha*, horn, dorsal, curving outward, and then inward, with tips crossed to each other. a. *P. mazavaloha*, horn, laterally going upwards with tips surpassing ½ eye diameter; body intermediate. b. *P. maingoka*, horn same orientation, but body flattened. Scale bars for A, B, C = 0.5 mm, all a, b = 0.5 mm.

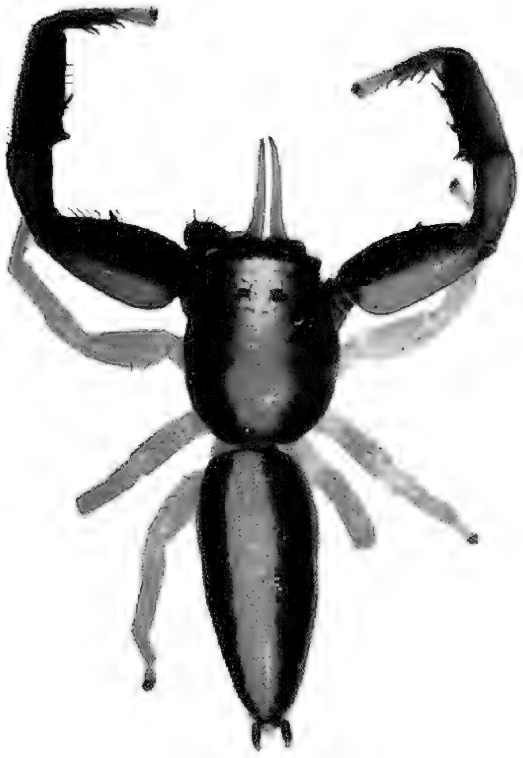


FIGURE 5. *P. cornuta*, habitus, dorsal. Scale = 1 mm.

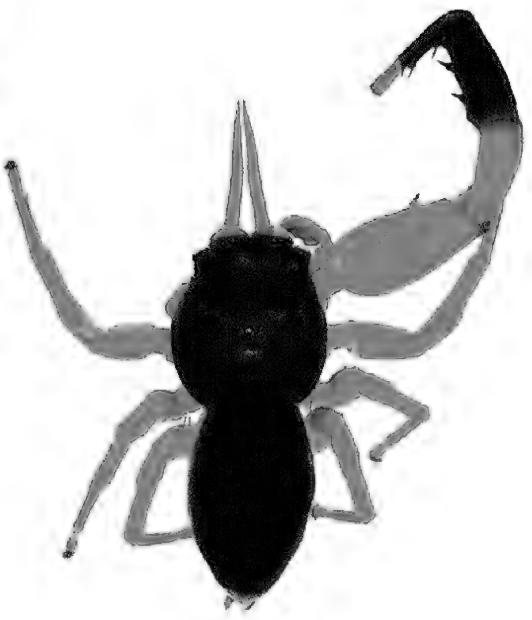


FIGURE 6. *P. manjelatra*, habitus, dorsal. Scale = 1 mm.

FIGURE 7. *P. lavatandroka*, habitus, dorsal. Scale = 1 mm.

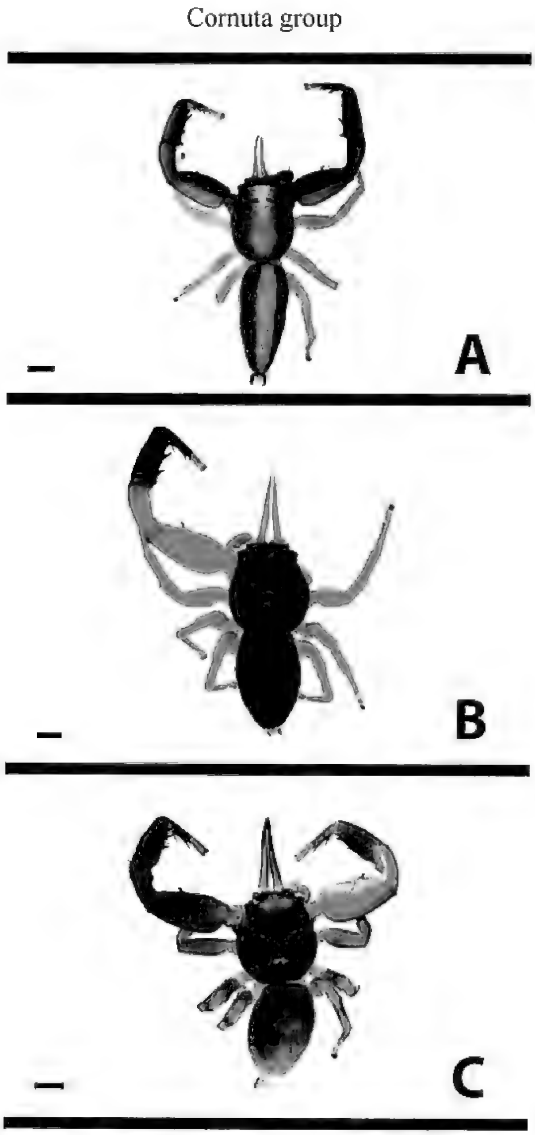


FIGURE 8. *Cornuta* group habitus, dorsal view. A. *P. cornuta*, habitus, dorsal. B. *P. manjelatra*, habitus, dorsal. C. *P. lavatandroka*, habitus, dorsal. Scale bars for A, B, C = 1 mm.

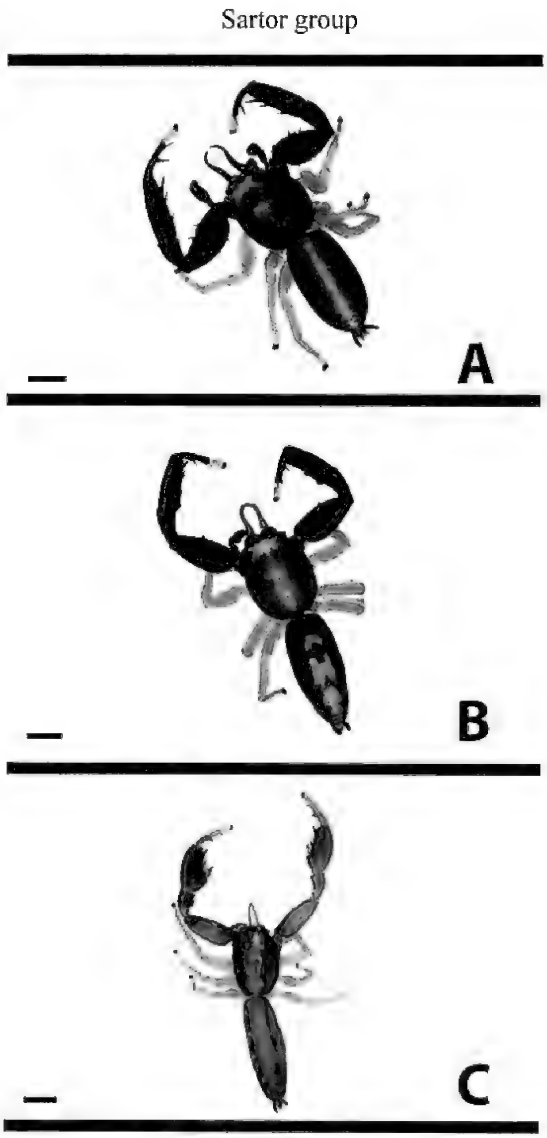


FIGURE 9. *Sartor* group habitus, dorsal view. A. *P. sartor*, habitus, dorsal. B. *P. mazavaloha*, habitus dorsal. C. *P. maingoka*, habitus, dorsal. Scale bars for A, B, C = 1 mm.

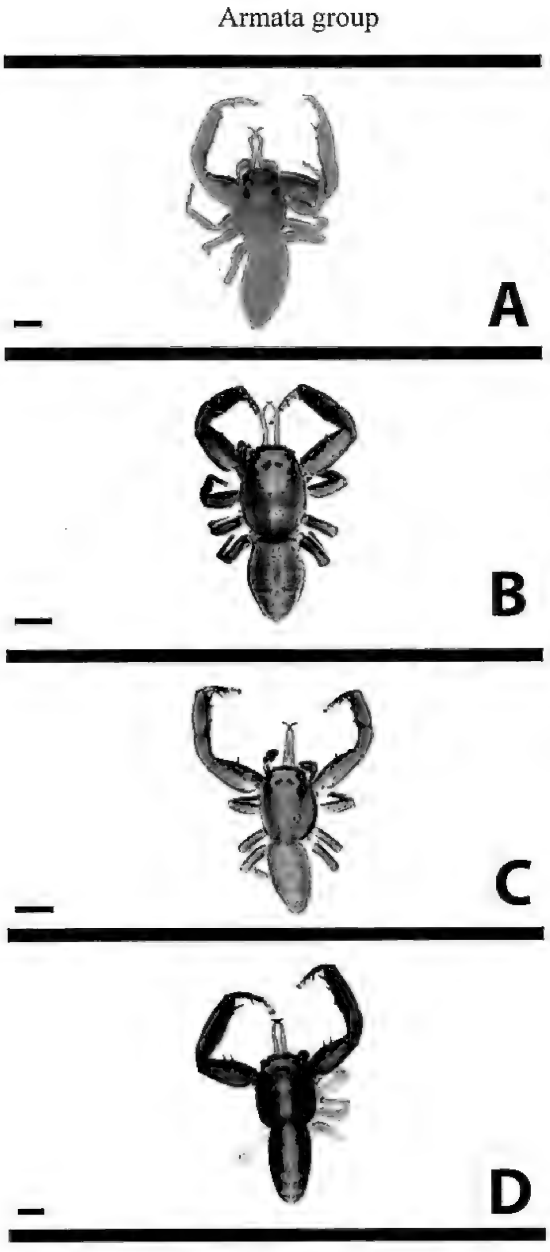


FIGURE 10. *Armata* group habitus, dorsal view. A. *P. armata*, habitus, dorsal. B. *P. griswoldi*, habitus, dorsal. C. *P. astina*, habitus, dorsal. D. *P. ombimanga*, habitus, dorsal. Scale bars for A, B, C, D = 1 mm.

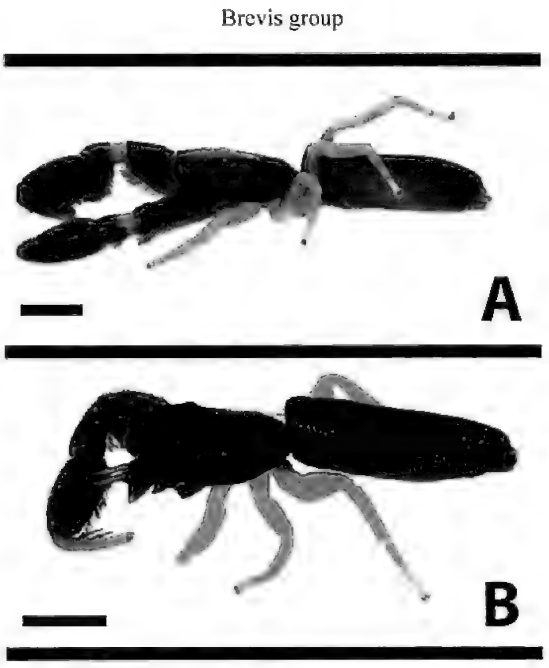


FIGURE 11. *Brevis* group, habitus, lateral view. A. *P. boritandroka*, habitus, lateral. B. *P. ngeroka*, habitus, lateral. Scale bars for A, B = 1 mm.

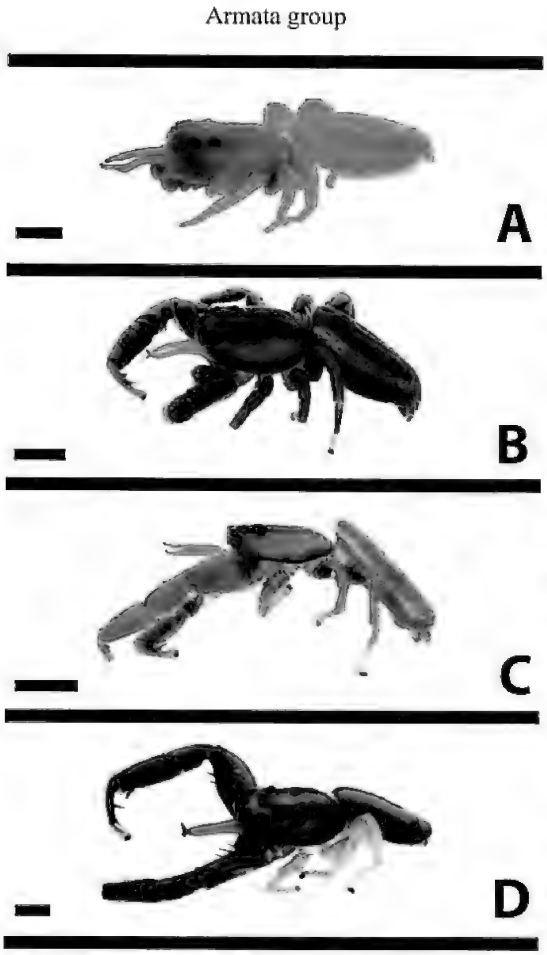


FIGURE 12. *Armata* group, habitus, lateral view. A. *P. armata*, habitus, lateral. B. *P. griswoldi*, habitus, lateral. C. *P. astina*, habitus, lateral. D. *P. ombimanga*, habitus, lateral. Scale bars for A, B, C, D = 1 mm.

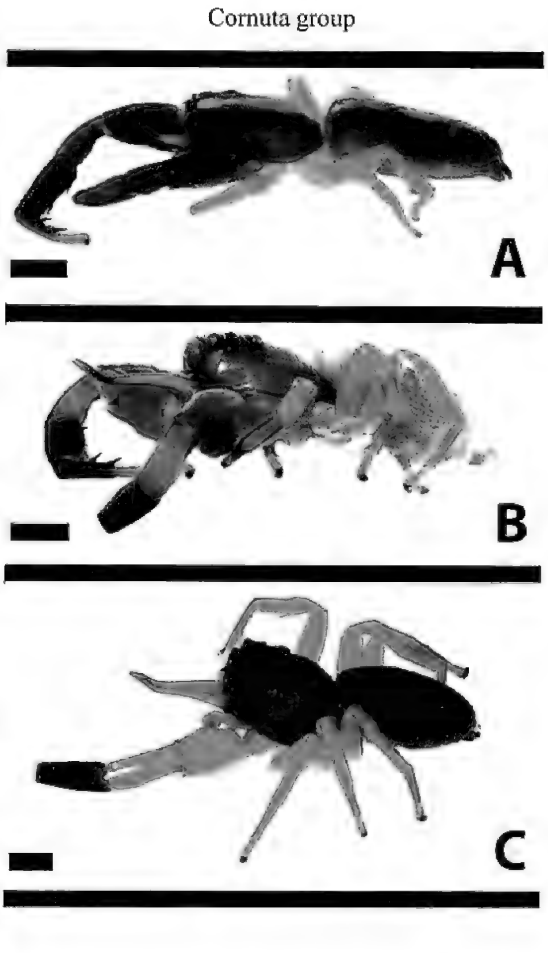


FIGURE 13. *Cornuta* group, habitus, lateral view. A. *P. cornuta*, habitus, lateral. B. *P. lavatandroka*, habitus, lateral. C. *P. manjelatra*, habitus lateral. Scale bars for A, B, C = 1 mm.

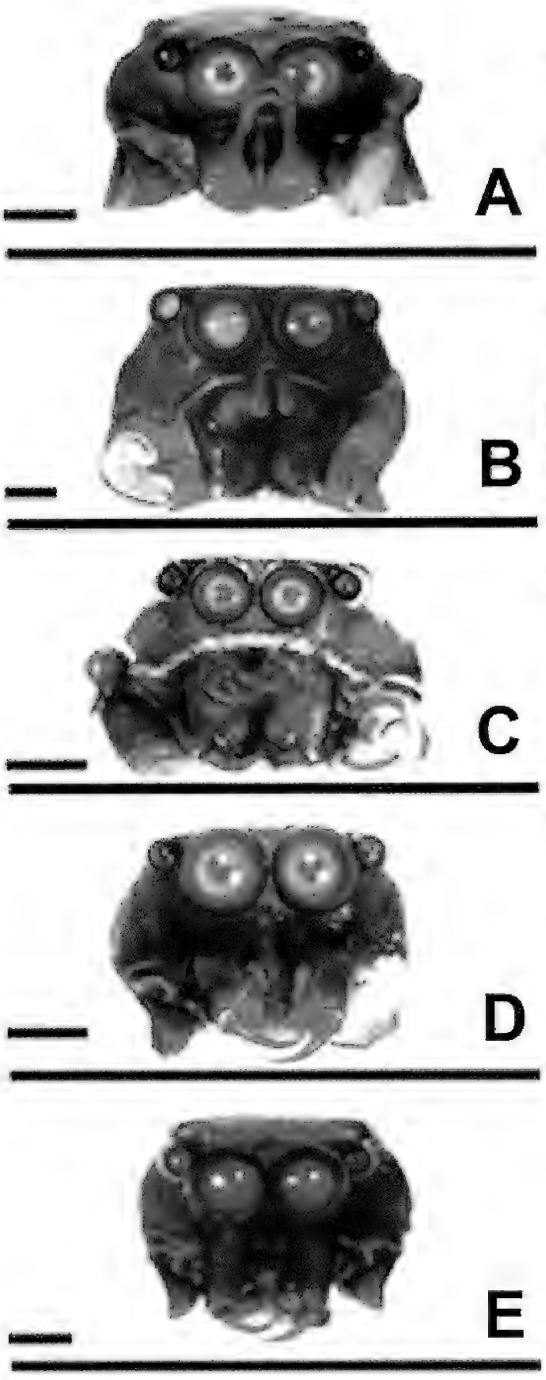


FIGURE 14. Male carapace, front view. A. *P. maingoka*, carapace, front. B. *P. lavatandroka*, carapace, front. C. *P. astina*, carapace, front. D. *P. ngeroka*, carapace, front. E. *P. boritandroka*, carapace, front. Scale bars for A, B, C, D, E = 0.35 mm.

Sartor group

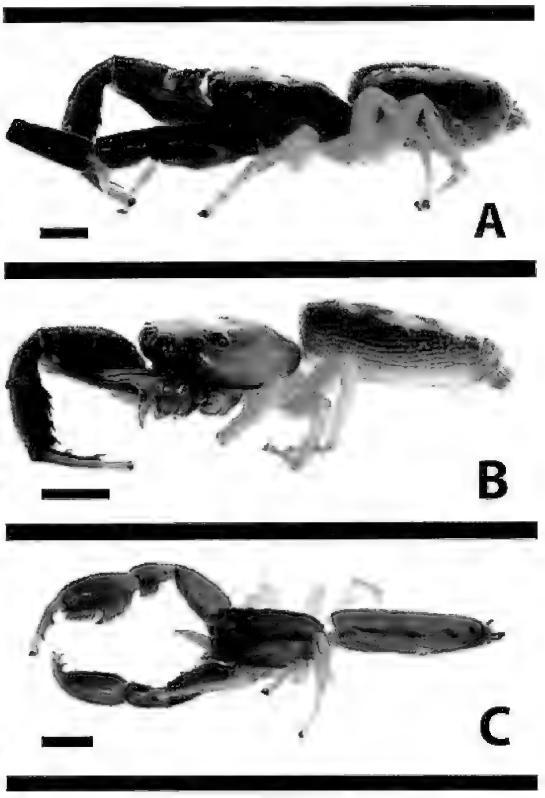


FIGURE 15. *Sartor* group, habitus, lateral view. A. *P. sartor*, habitus, lateral. B. *P. mazavaloha*, habitus, lateral. C. *P. maingoka*, habitus, lateral. Scale bars for A, B, C = 1 mm.

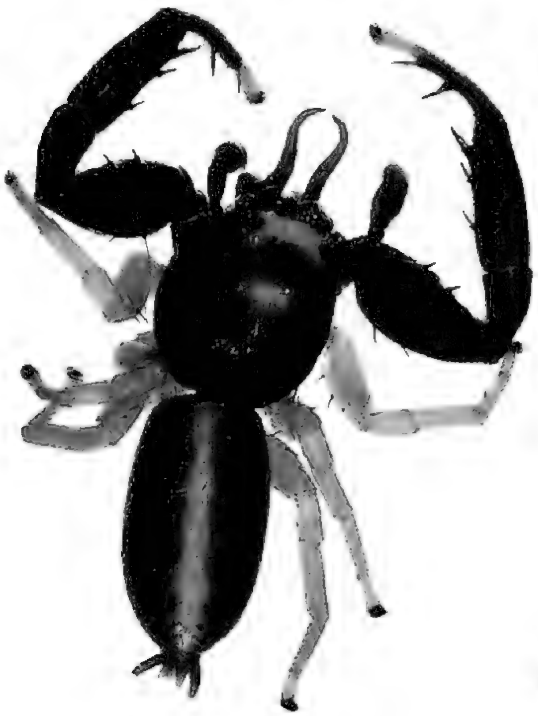


FIGURE 16. *P. sartor*, habitus, dorsal. Scale bar = 1 mm.

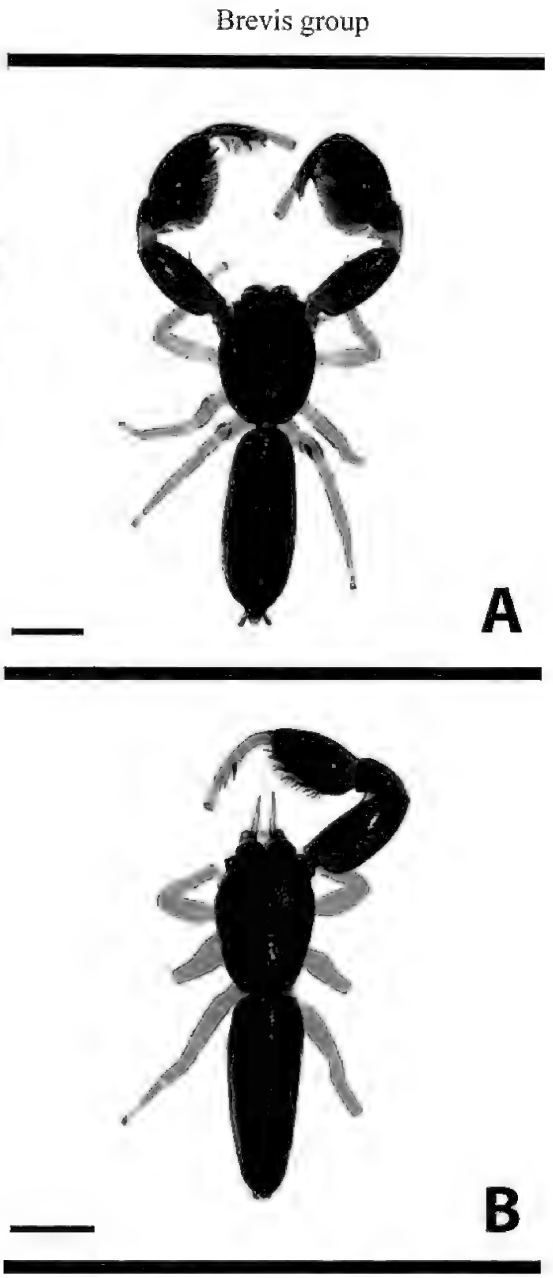


FIGURE 17. *Brevis* group, habitus, dorsal view. A. *P. boritandroka*, habitus, dorsal. B. *P. ngeroka*, habitus, dorsal. Scale bars for A, B = 1 mm.

FIGURE 18. *P. armata*, habitus, dorsal. Scale bar = 1 mm.

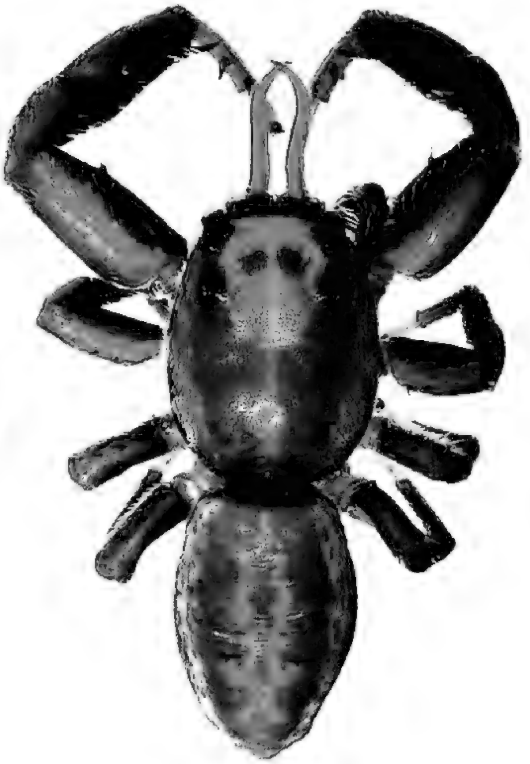


FIGURE 19. *P. griswoldi*, habitus, dorsal. Scale bar = 1 mm.

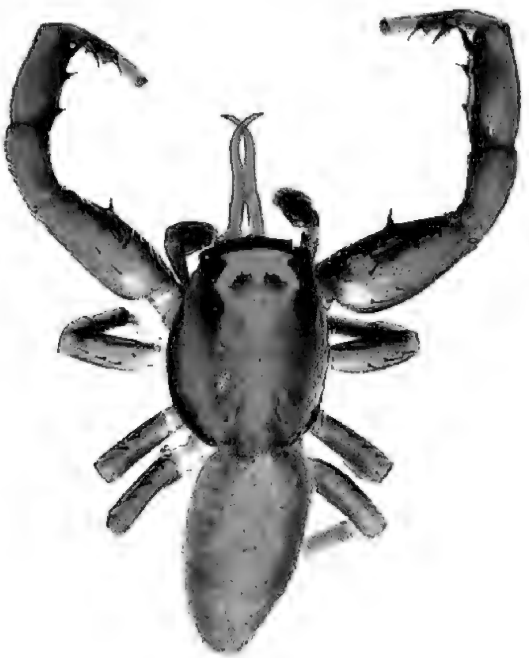


FIGURE 20. *P. astina*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 21. *P. ombimanga*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 22. *P. mazavaloha*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 23. *P. maingoka*, habitus, dorsal. Scale bar = 1 mm.

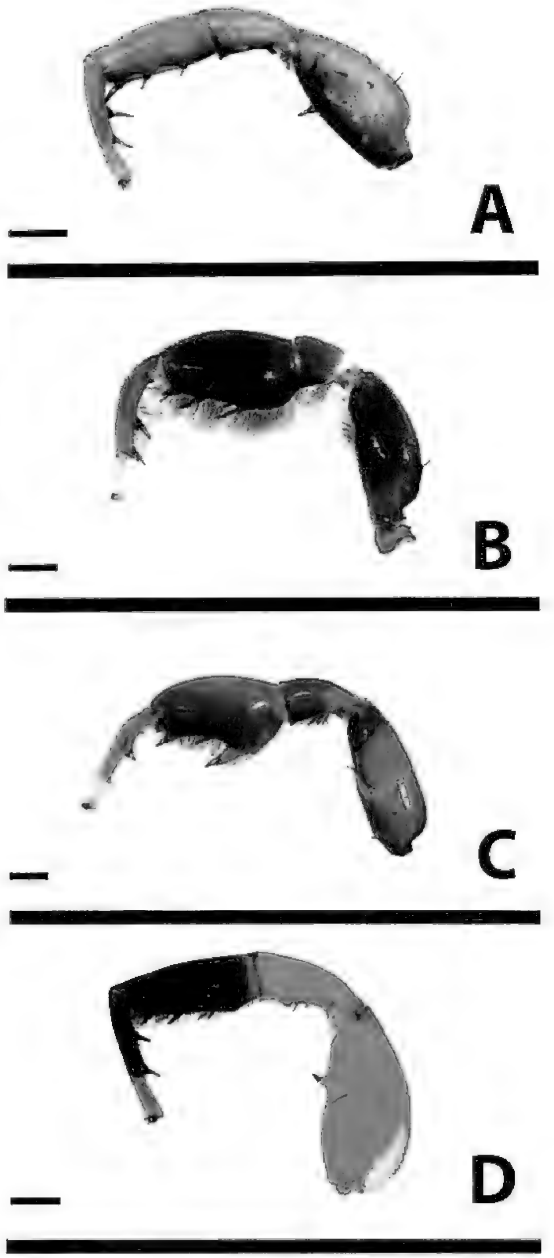


FIGURE 24. *Padilla* front legs, dorsal view. A. *P. astina*, leg I, dorsal. B. *P. boritandroka*, leg I, dorsal. C. *P. maingoka*, leg I, dorsal. D. *P. manjelatra*, leg I, dorsal. Scale bars for all = 0.5 mm.

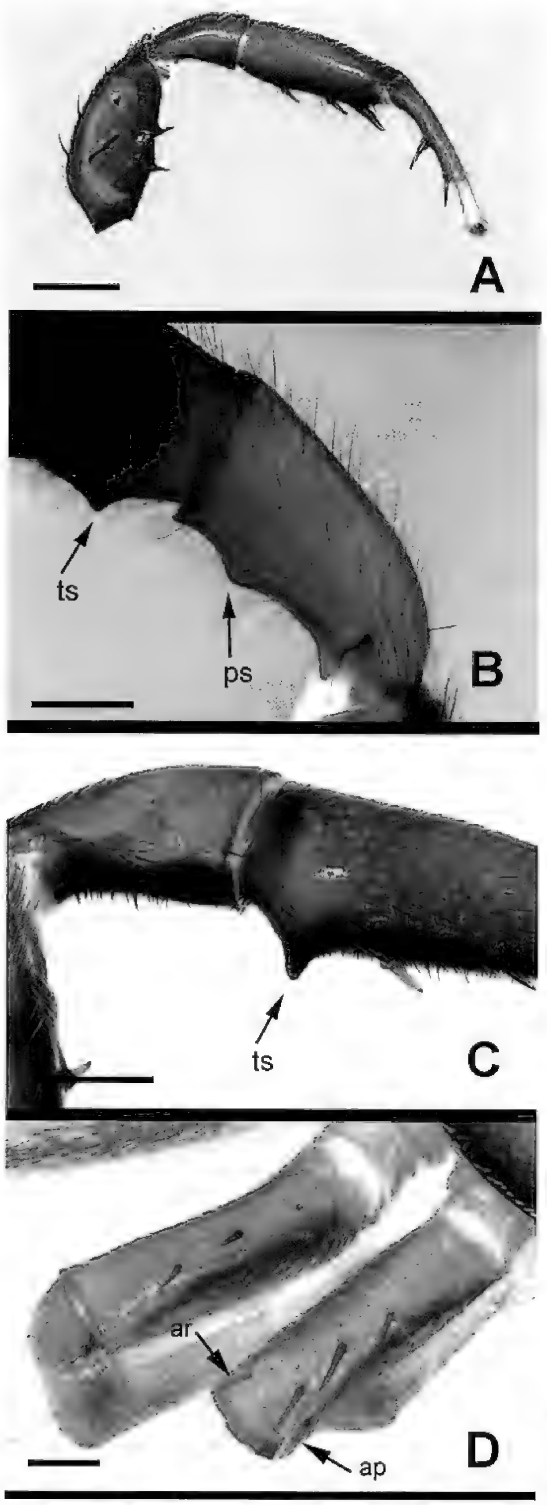


FIGURE 25. *Padilla* leg spinations. A. *P. sartor*, femur I, two proventral spines. B. *P. manjelatra*, Tb1 and Pt1 spurs. C. *P. cornuta*, Tb1 spur. D. *P. griswoldi*, F3 and F4 1/1/1 dorsal spine arrangement, additional promarginal and retromarginal spine. Scale bars for A = 1 mm, B, C = 0.5 mm, D = 0.2 mm.

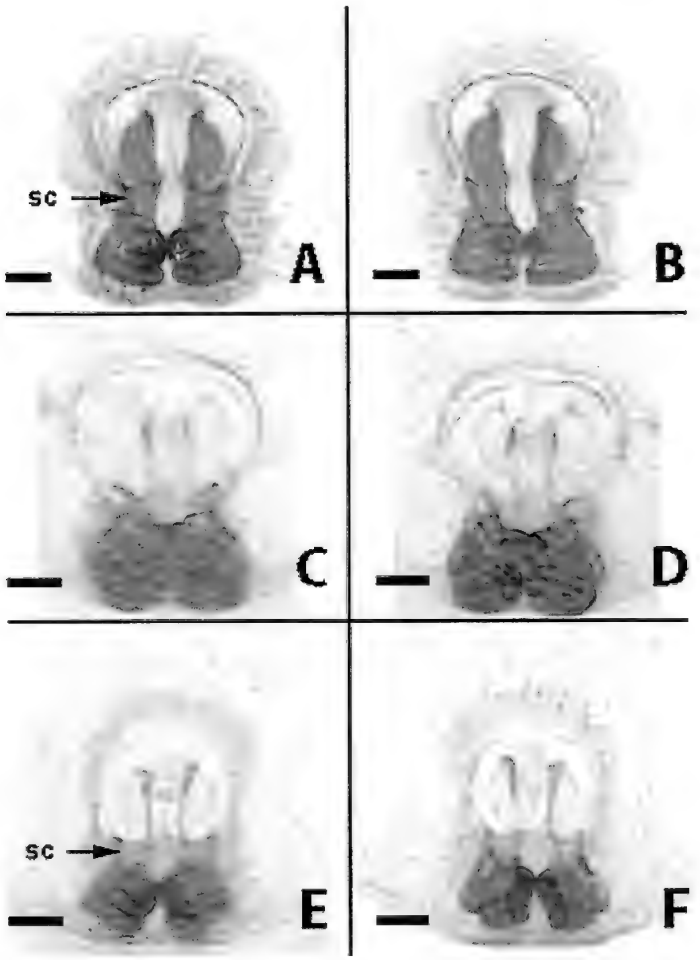


FIGURE 26. *Padilla* female epygina. A. *P. mitohy*, epyginum, ventral. B. epyginum, dorsal. C. *P mihaingo*, epyginum, ventral. D. epyginum, dorsal. E. *P. foty*, epyginum, ventral. F. epyginum, dorsal. Scale bars for A, B, C, D, E, F = 0.2 mm.

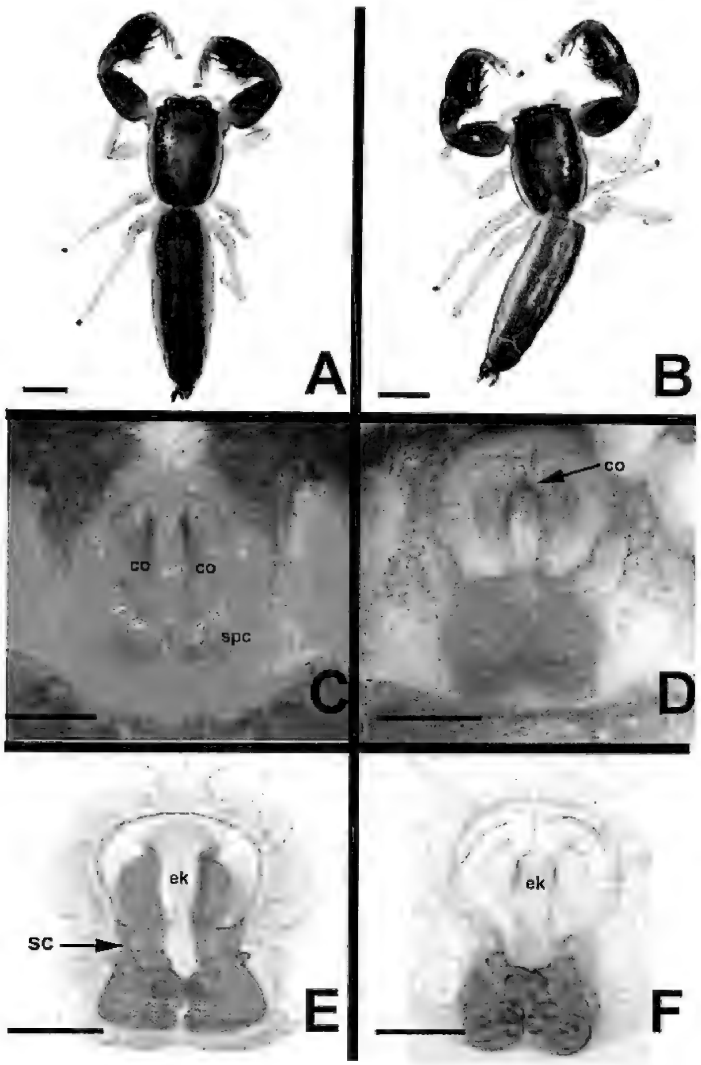


FIGURE 27. *P. mitohy*, *P. mihaingo*, habitus, dorsal, epyginum. A. *P. mitohy*, habitus, dorsal. B. *P. mihaingo*, habitus, dorsal. C. *P. mitohy* epyginum, ventral. D. *P. mihaingo*, epyginum, ventral. E. *P. mitohy*, epyginum, dorsal. F. *P. mihaingo*, epyginum, dorsal. Scale bars for A, B = 1 mm, C, D = 0.3 mm, E, F = 0.2 mm.

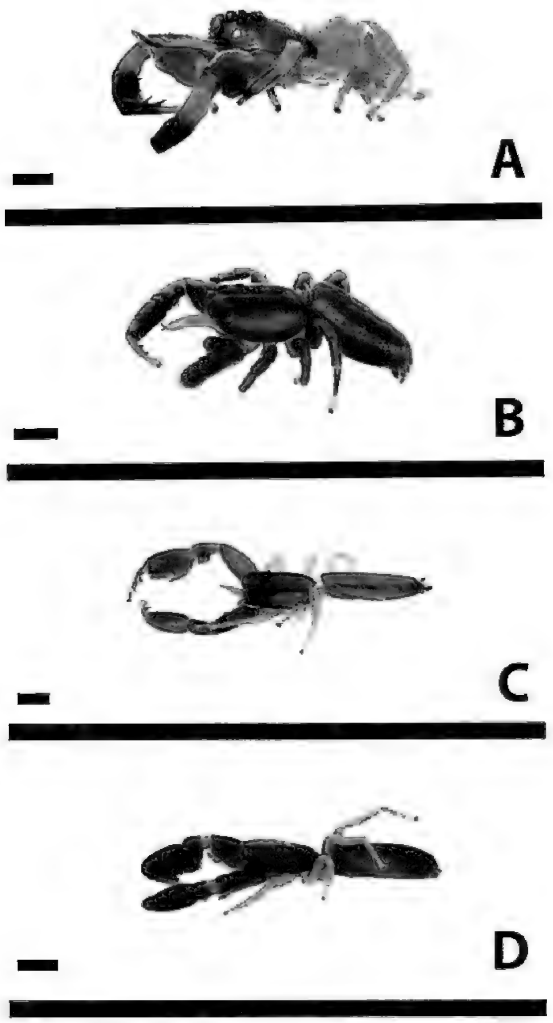


FIGURE 28. Male habitus, lateral view showing the difference in body shape and carapace height. A. *P. lavatandroka*, habitus, lateral ("hopper"). B. *P. griswoldi*, habitus, lateral ("intermediate"). C. *P. maingoka*, habitus, lateral. D. *P. boritandroka*, habitus, lateral (both "runner"). Scale bars for A, B, C, D = 1 mm.

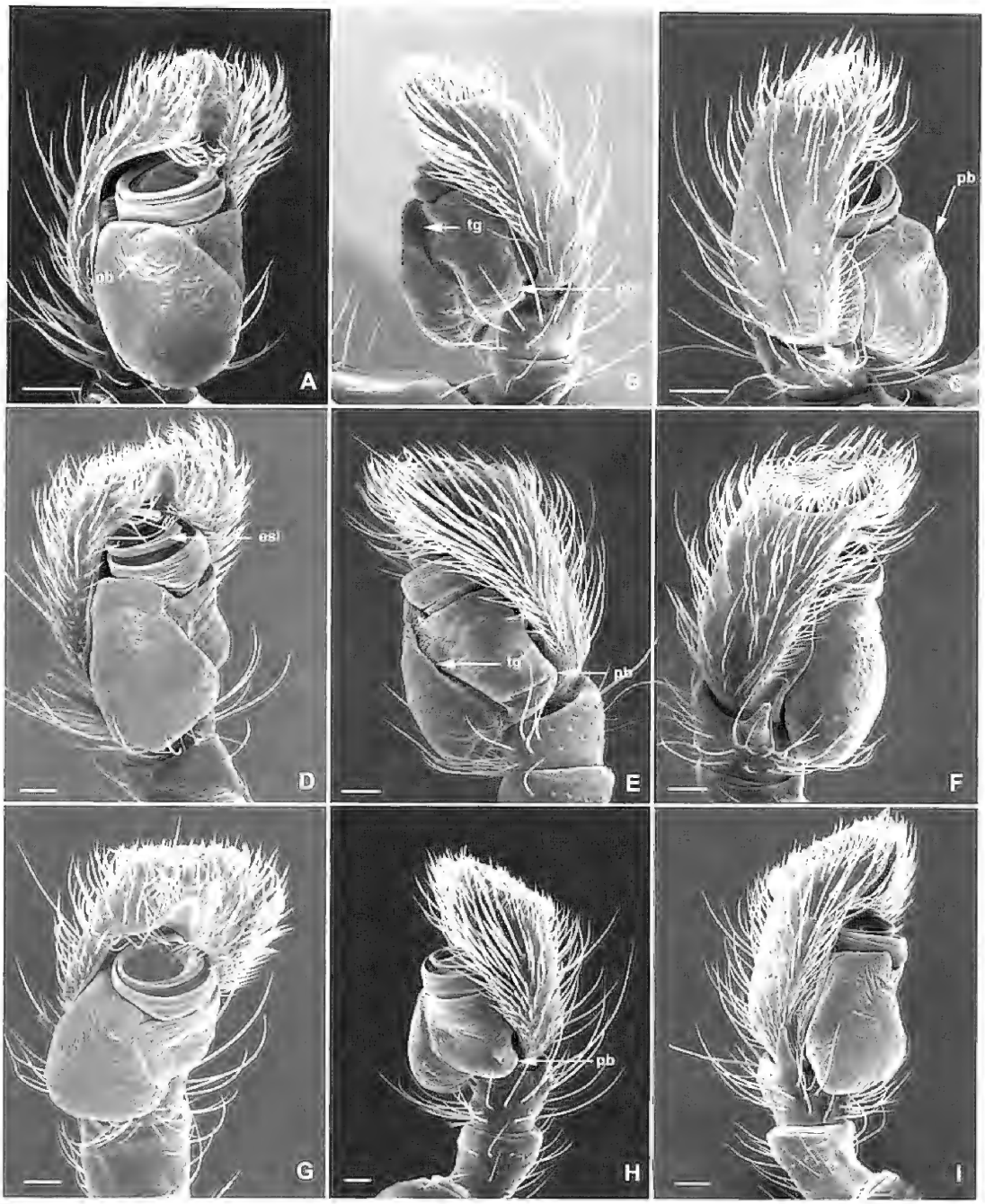


FIGURE 29. *Cornuta* group palps. A. *P. cornuta*, right palp, ventral. B. prolateral. C. retrolateral. D. *P. manjelatra*, right palp, ventral. E. palp, prolateral. F. palp, retrolateral. G. *P. lavatandroka*, right palp, ventral. H. palp, prolateral. I. palp, retrolateral. Scale bars C = 30 µm, A, E, F = 20 µm, B , D, G, H, I = 10 µm.

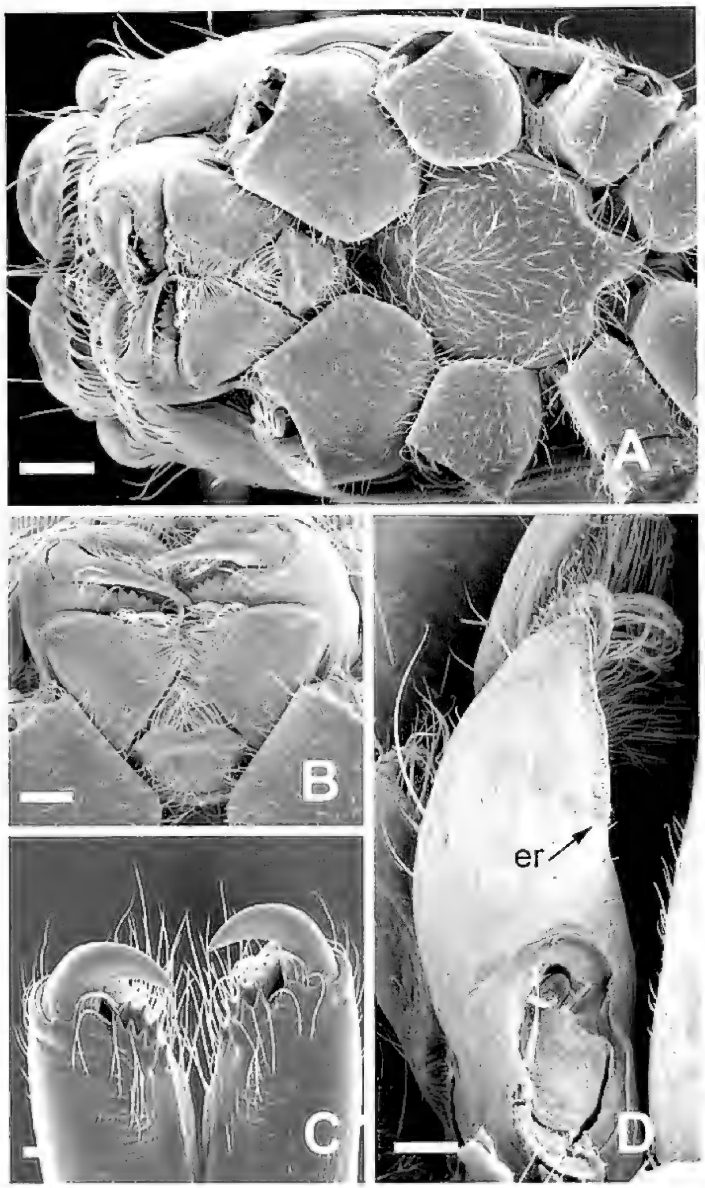


FIGURE 30. *Padilla* mouth parts. A. *P. lavatandroka*, sternum. B. endites, labium, teeth, fangs. C. teeth, fangs, retromargin. D. endite, serrula extending till the base of endite. Scale bars for A = 200 µm, B, C, D = 100 µm.

FIGURE 31. *Sartor* group palps. A. *P. sartor*, right palp, ventral. B. prolateral. C. retrolateral. D. *P. mazavaloha*, left palp, ventral. E. prolateral. F. retrolateral. G. *P. maingoka*, right palp, ventral. H. prolateral. I. retrolateral. Scale bars for A, B, C = 100 µm, D, E, F, G, H, I = 30 µm.

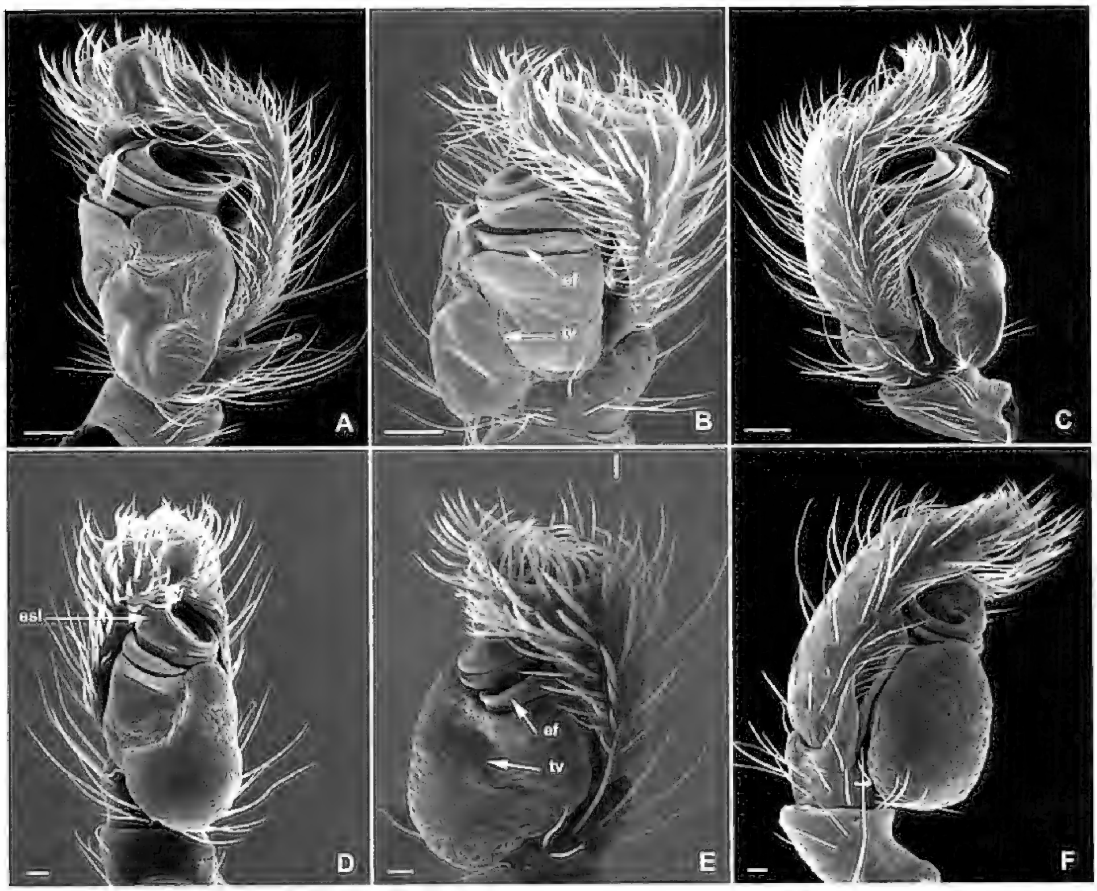


FIGURE 32. *Brevis* group palps. A. *P. boritandroka*, left palp, ventral. B. prolateral. C. retrolateral. D. *P. ngeroka*, left palp, ventral. E. prolateral. F. retrolateral. Scale bars for all = 0.2 mm.

FIGURE 33. *Armata* group palps. A. *P. griswoldi*, right palp, ventral. B. prolateral. C. retrolateral. D. *P. astina*, left palp ventral. E. prolateral. F. retrolateral. G. *P. ombimanga*, right palp, ventral. H. prolateral. I. retrolateral. Scale bars for A, B, C = 30 µm, D, E, F = 20 µm, G, H, I = 10 µm.

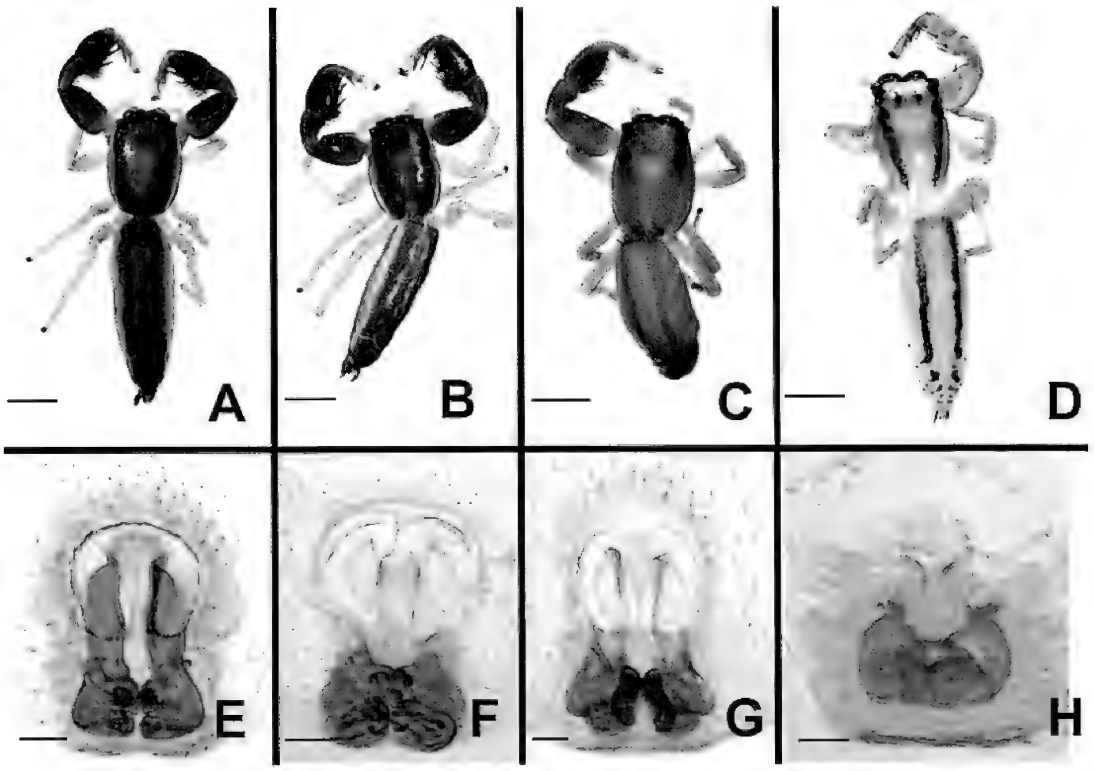


FIGURE 34. Female *Padilla* habitus, dorsal view, epygina dorsal view. A. *P. mitohy*, habitus dorsal. E. epyginum, dorsal. B. *P. mihaingo*, habitus, dorsal. F. epyginum, dorsal. C. *P. foty*, habitus dorsal. G. epyginum, dorsal. D. *P. ngeroka*, habitus dorsal. H. epyginum, dorsal. Scale bars for A, B, C = 1 mm, D, E, F, G, H = 0.2 mm.

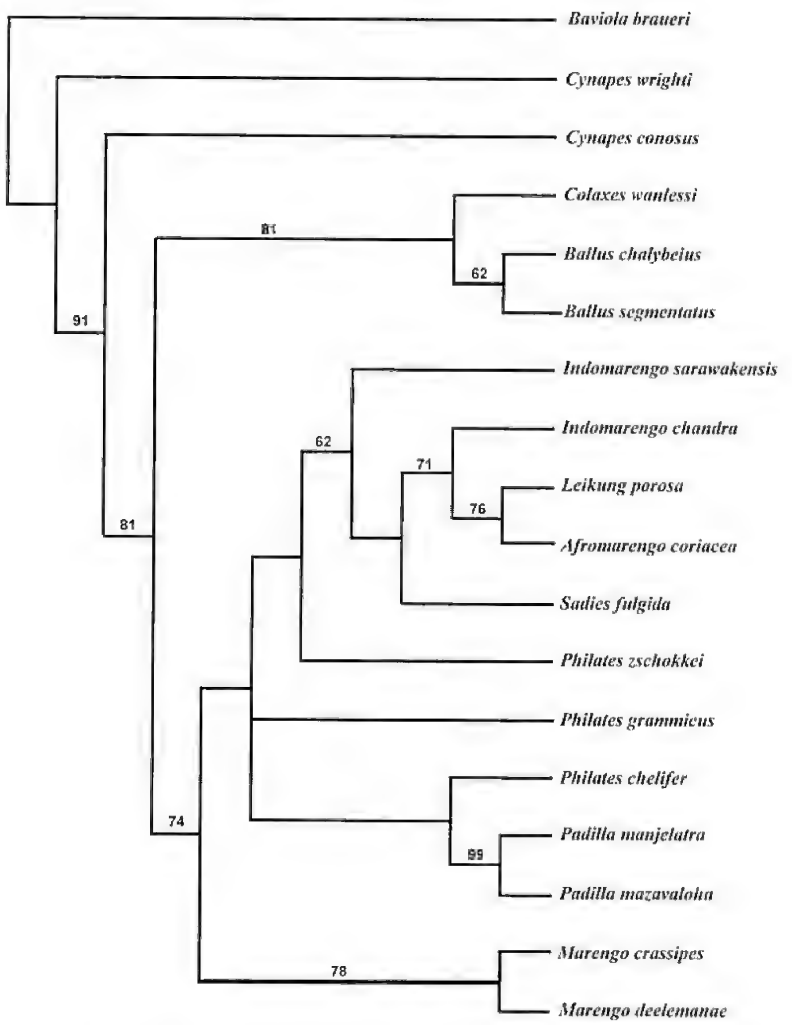


FIGURE 35. Placements of *Padilla* within the Ballinae morphology cladogram (Benjamin, 2004) based on parsimony analysis of 42 morphological characters. Strict consensus of 3 most parsimonious trees. L = 40.68, CI = 0.77, RI = 0.83, HI= 0.22.

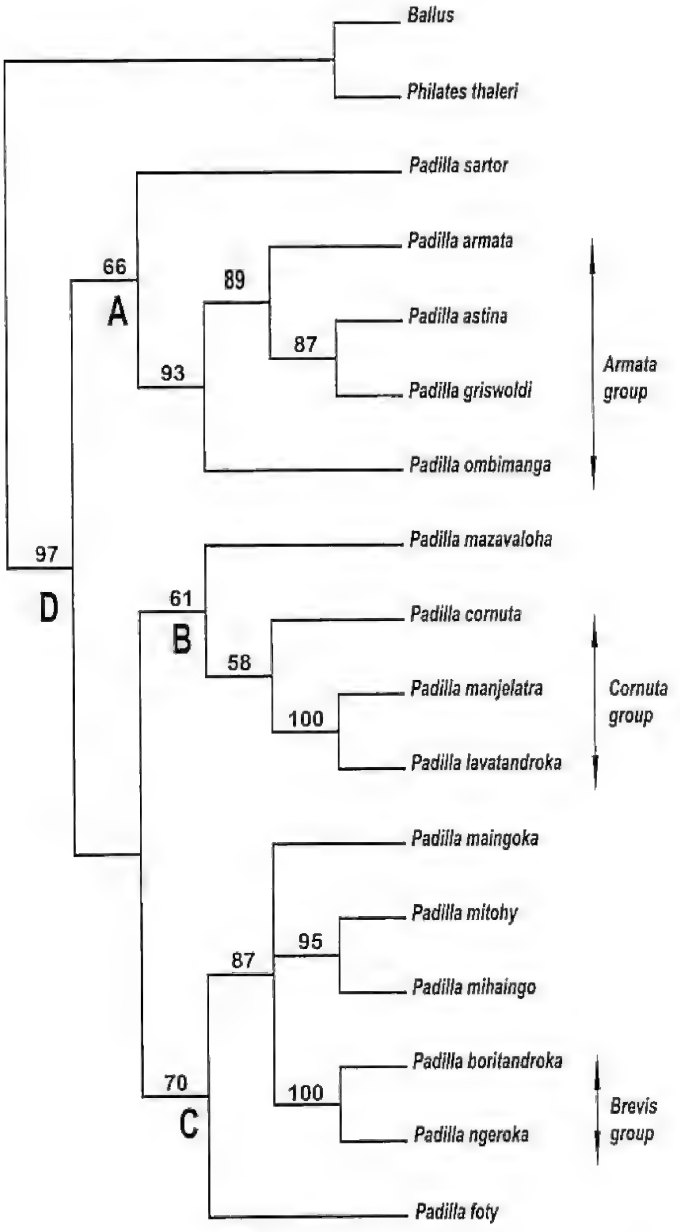


FIGURE 36. Phylogenetic relationships among *Padilla* species based on parsimony analysis of 38 morphological characters. Strict consensus of 3 most parsimonious trees, L = 33.74, CI = 0.82, RI = 0.89, HI = 0.17. Bootstrap values are shown in bold below branches on the cladogram.

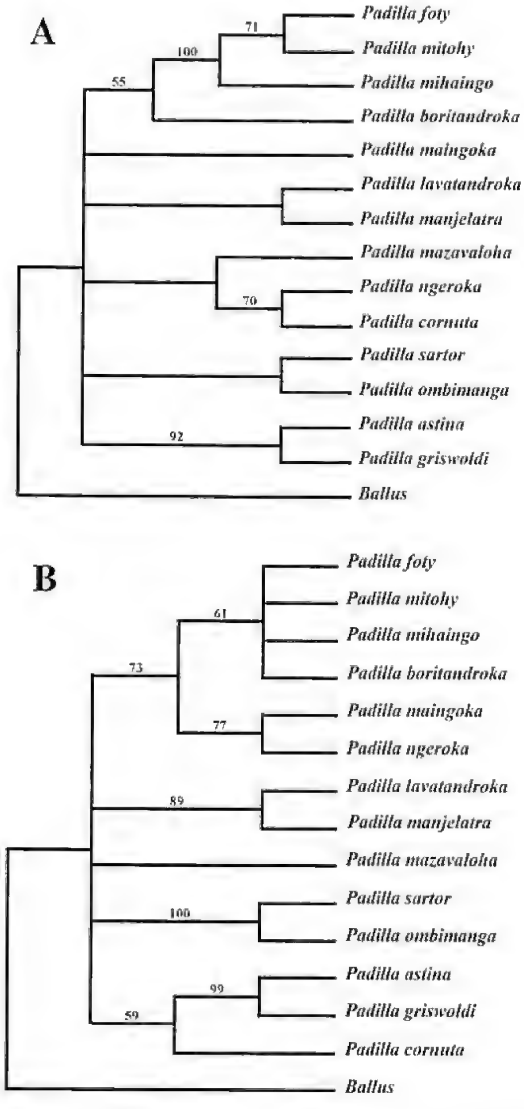


FIGURE 37. Phylogenetic relationships among *Padilla* species based on parsimony. A. analysis of 378 bp of COI gene. Strict consensus of 5 most parsimonious trees. L= 215, CI = 0.61, RI = 0.58. B. analysis of 759 bp of 28S gene. Strict consensus of 2 most parsimonious trees. L= 165, CI = 0.77, RI = 0.71. Bootstrap values are shown in bold below branches on the cladogram.

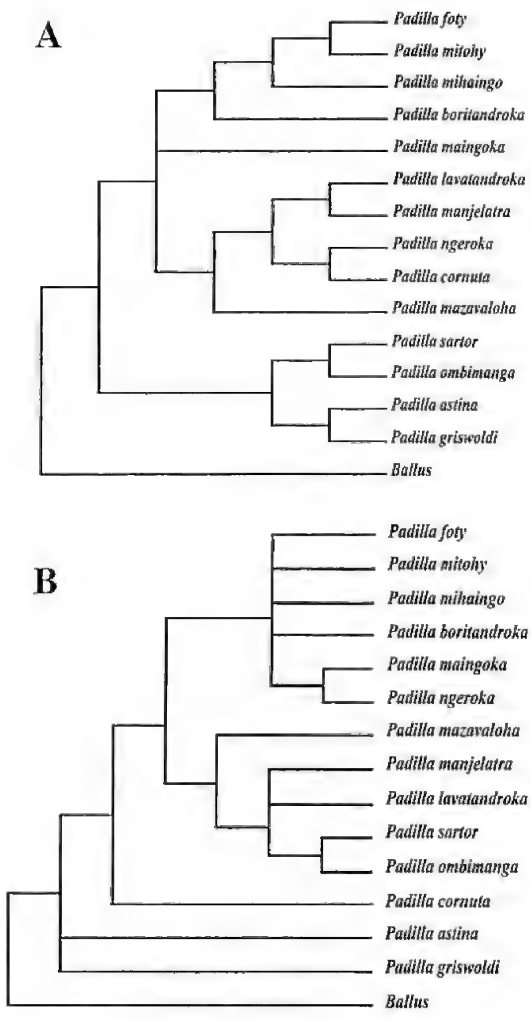


FIGURE 38. Phylogenetic relationships among *Padilla* species based on maximum likelihood analysis using GTR+I+G model, phylogeny from: A. COI gene, 1 tree, –ln L= 1614.30907. B. 28S gene, strict consensus of 6 trees, –ln L= 1879.24764

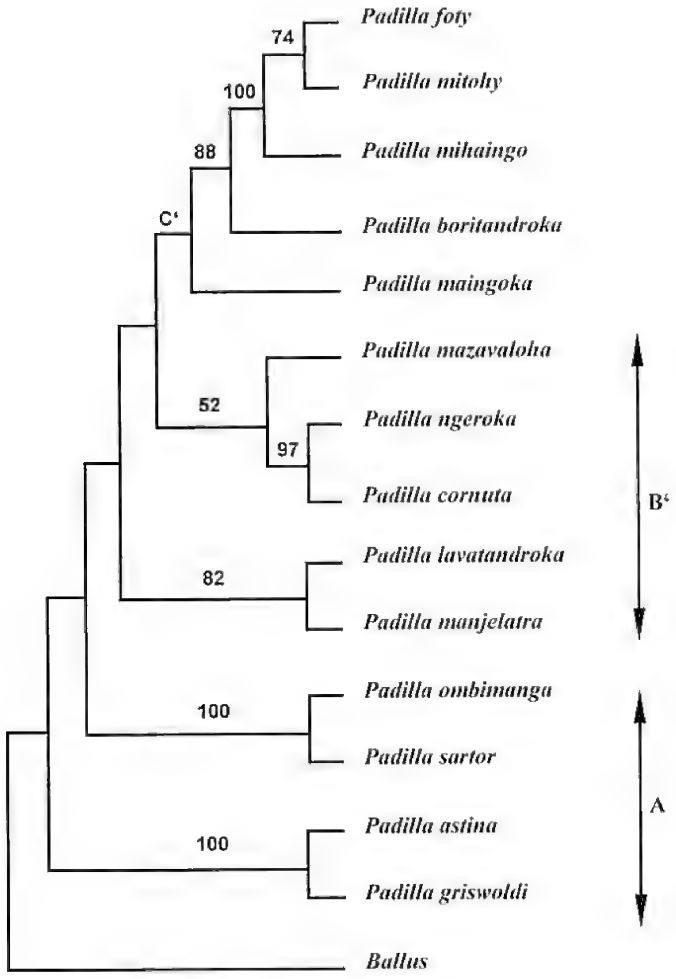


FIGURE 39. Phylogenetic relationships among *Padilla* species based on parsimony analysis of the combained 1137 bp of COI and 28S genes. One tree of L= 436, CI= 0.64, RI= 0.58.

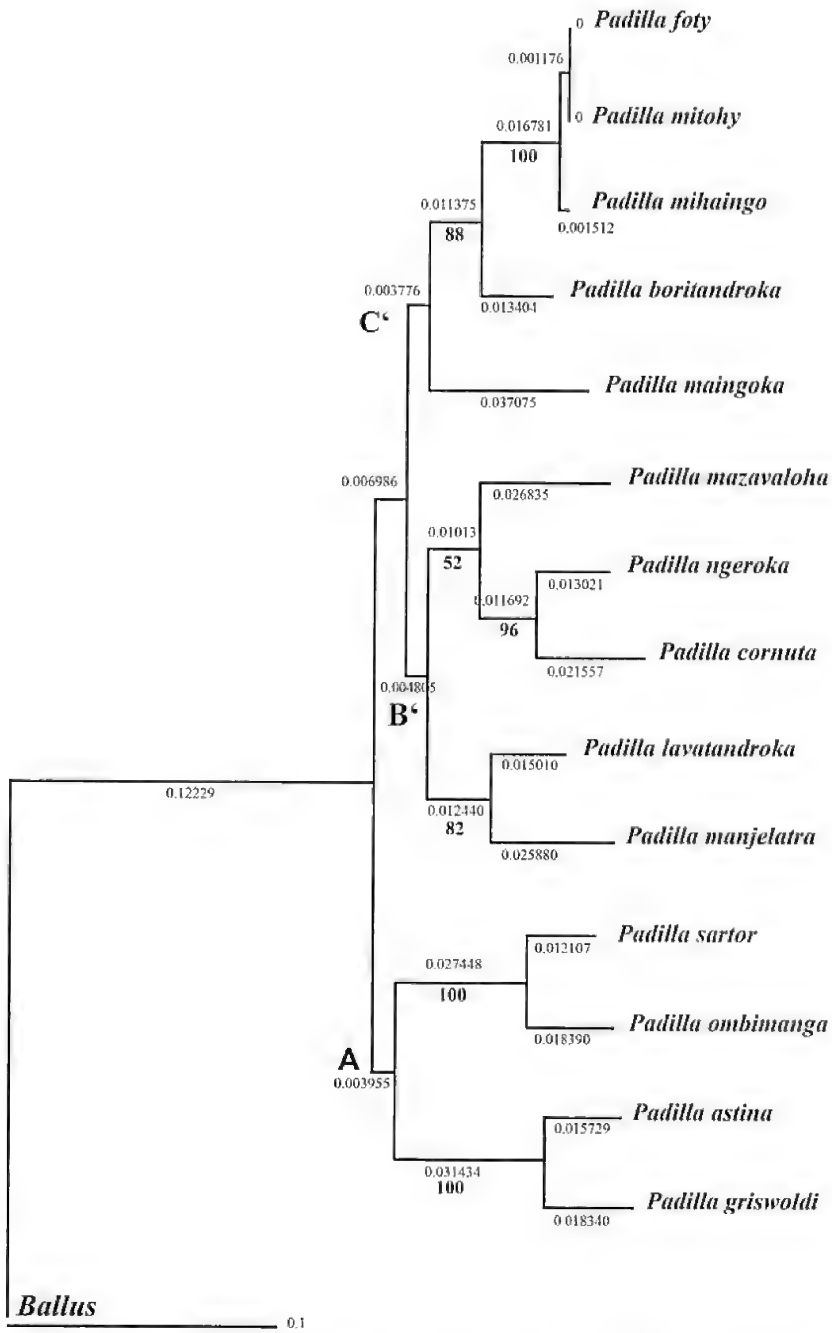


FIGURE 40. Phylogenetic relationships among *Padilla* species based on maximum likelihood analysis using GTR+I+G model, phylogeny from the combained 1137 bp of COI and 28 genes. One tree, -ln L = 3771.21431.

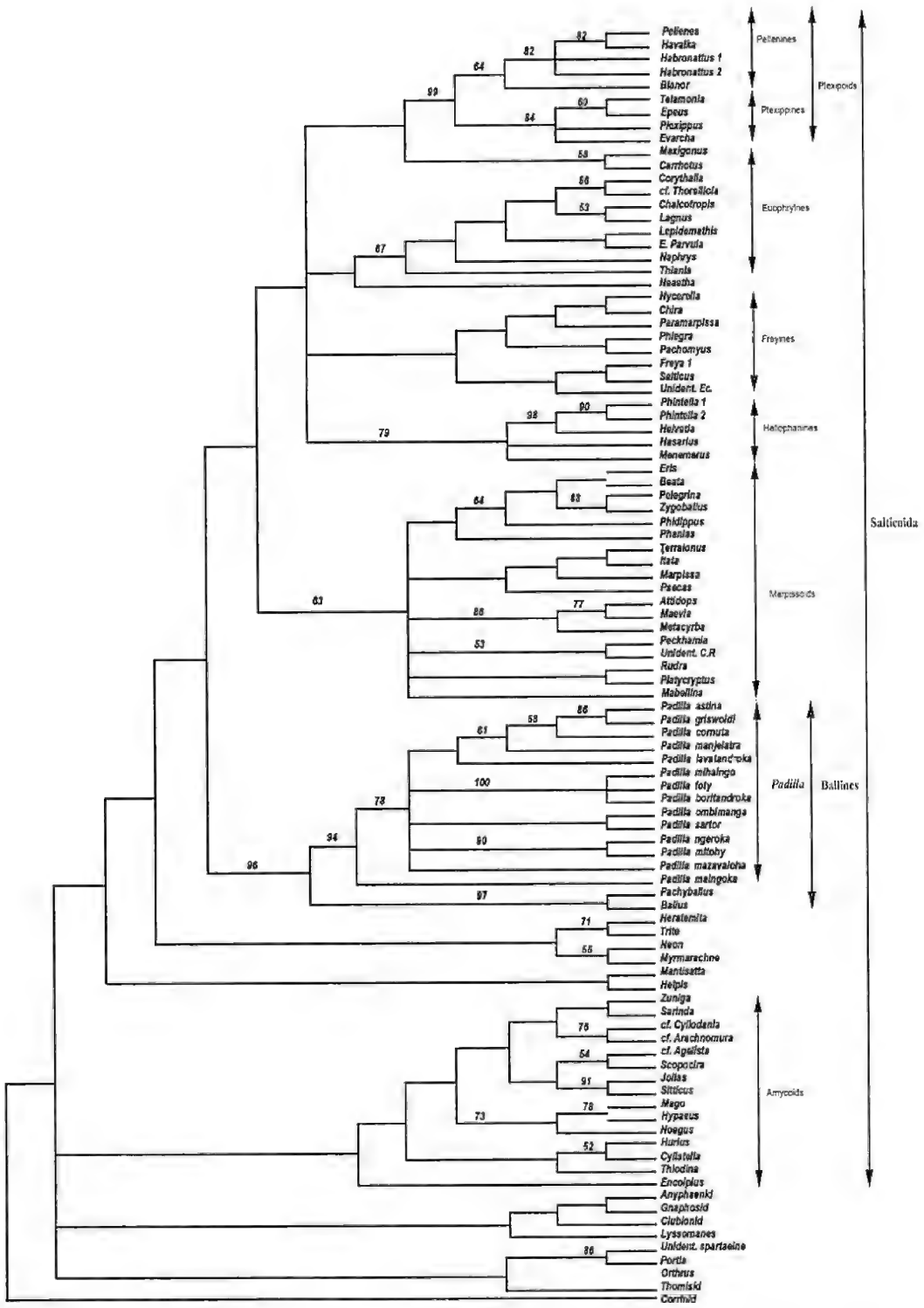


FIGURE 41. Placement of *Padilla* within the 28S Salticidae phylogeny (Hedin and Maddison 2003). Analysis based on parsimony, 35 most parsimonious trees, L= 5222.

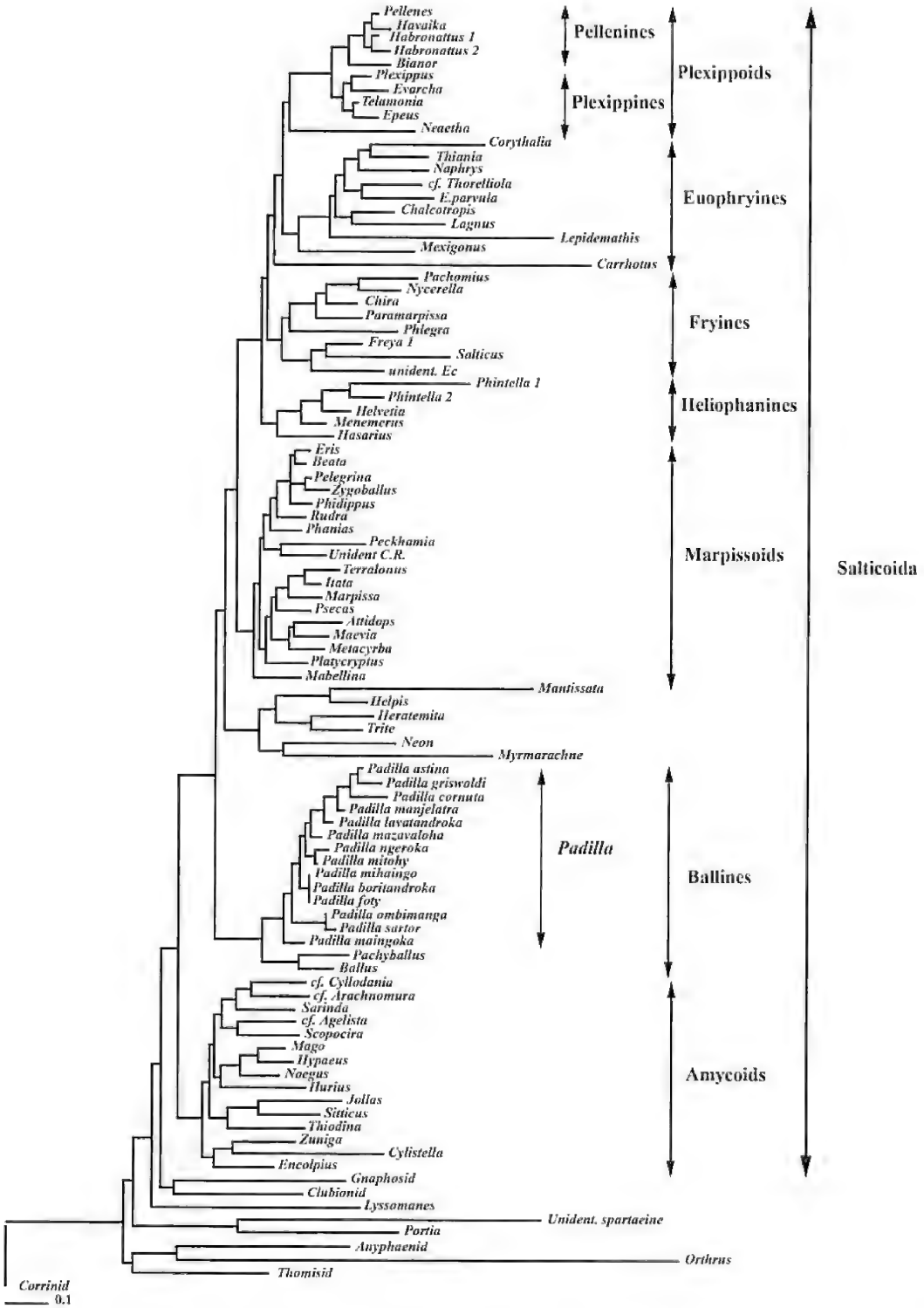


FIGURE 42. Placement of *Padilla* within the 28S Salticidae phylogeny (Hedin and Maddison 2003). Analysis based on maximum likelihood using GTR+G+I model. 1 tree, -ln L = 22284.10856.

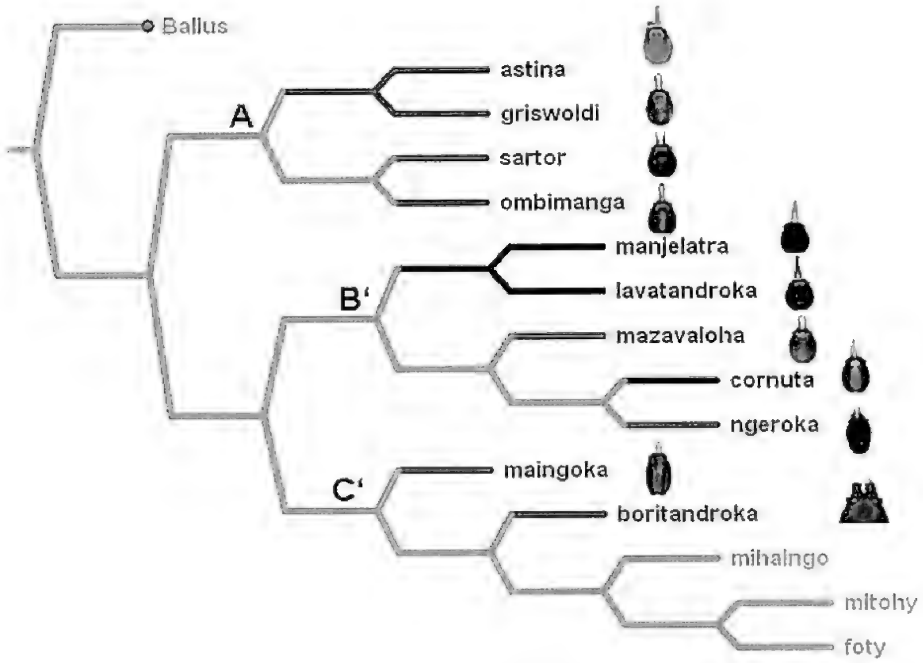


FIGURE 43. Horn curvature mapped on the combained COI and 28S maximum likelihood phylogeny. Convergent evolution of the horn in *Padilla*. Key: Armata group, blue; Sartor group, red; Cornuta group, black; Brevis group, green; unassigned and outgroup, purple.

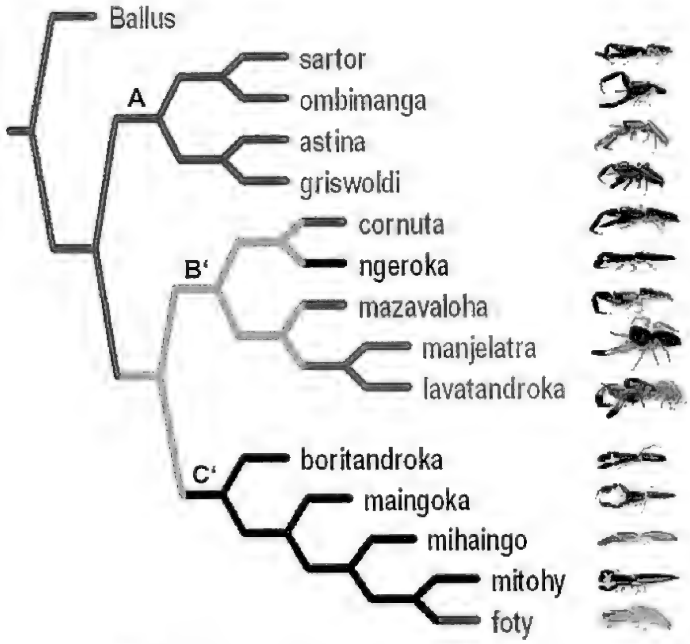


FIGURE 44. Body shape and life styles mapped on the combained COI and 28S maximum likelihood phylogeny. Convergent evolution of the body shape in *Padilla*. Key: elongate-intermediate, green; beetle-like intermediate, blue; scorpion-like runners, black; protruding hoppers, red.

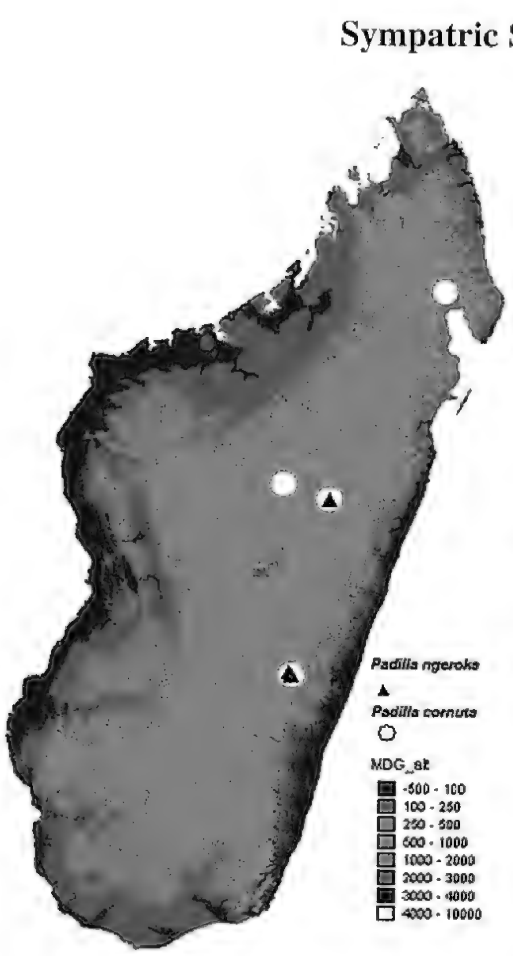


FIGURE 45. Altitudinal distribution map for *P. cornuta* and *P. ngeroka* clade.

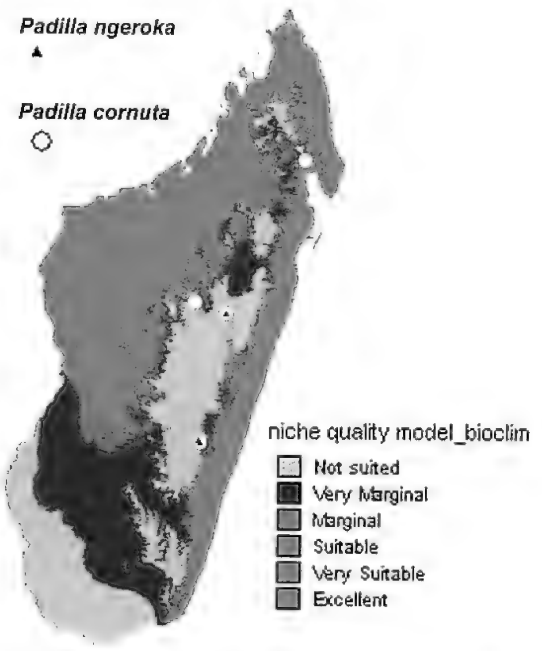


FIGURE 46. *P. ngeroka, P. cornuta* niche quality map.

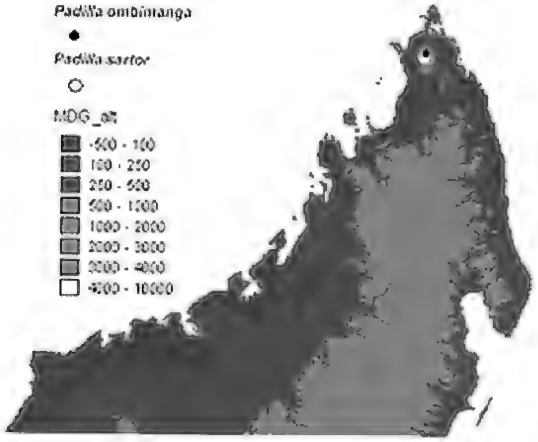


FIGURE 47. Altitudinal distribution map for *P. sartor* and *P. ombimanga* clade.

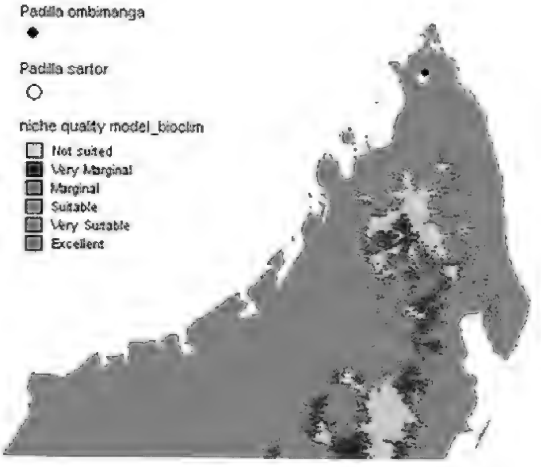


FIGURE 48. *P. sartor, P. ombimanga* niche quality map.

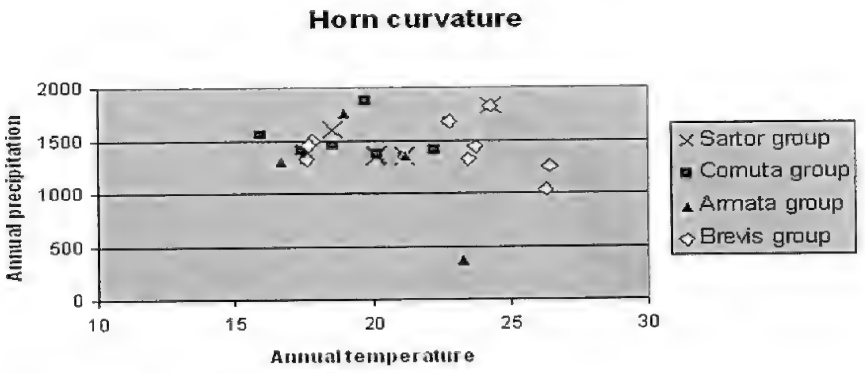


Figure 69A

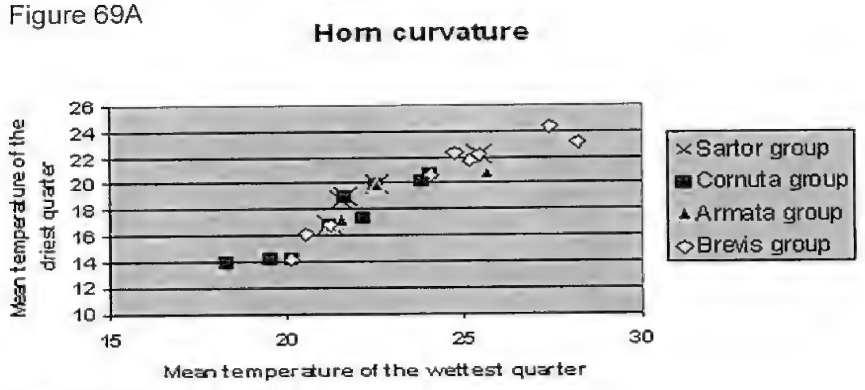


Figure 69B

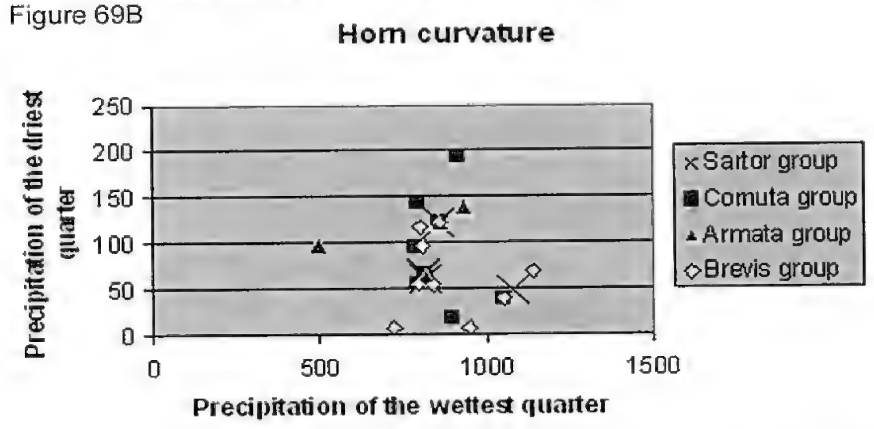


FIGURE 49. Correlation of "horn curvature", temperature and precipitation. A. Horn curvature, annual temperature, annual precipitation. B. Horn curvature, mean temperature of the wettest quarter, mean temperature of the driest quarter. C. Precipitation of the wettest quarter, precipitation of the driest quarter.

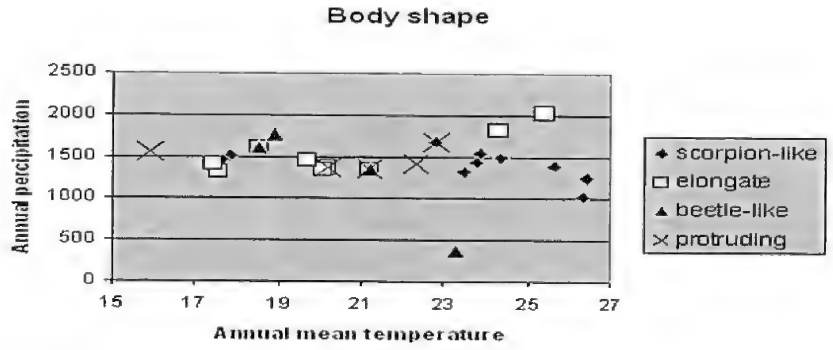


Figure 70A

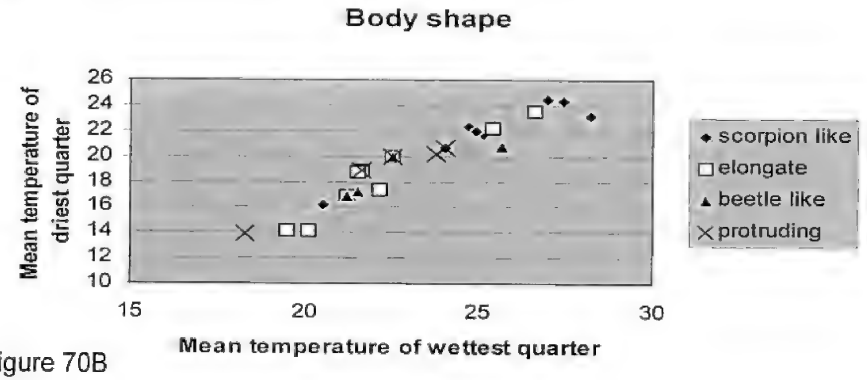


Figure 70B

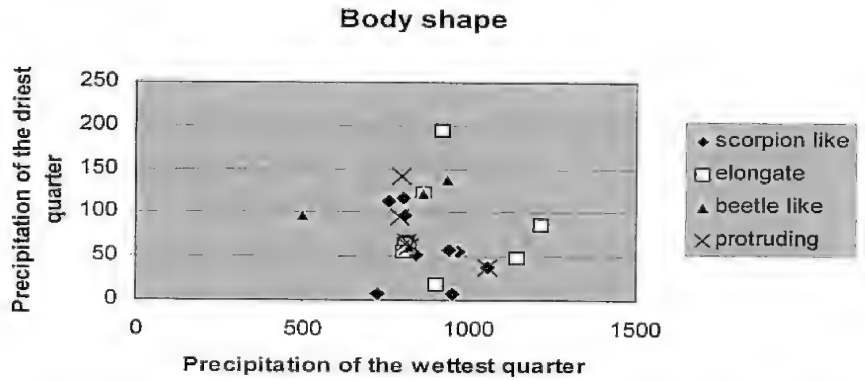


FIGURE 50. Correlation of "body shape", temperature and precipitation. A. Body shape, annual temperature, annual precipitation. B. Body shape, mean temperature of the wettest quarter, mean temperature of the driest quarter. C. Body shape, precipitation of the wettest quarter, precipitation of the driest quarter.

FIGURE 51. Distribution map for *Padilla* species in Madagascar. The dots represent places were species were found.

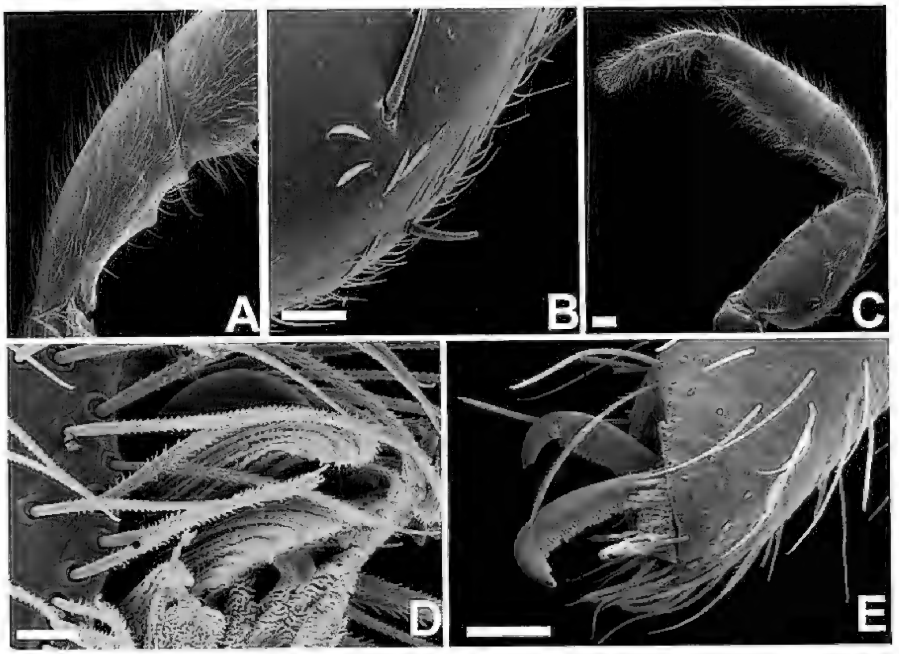


FIGURE 52. *Padilla* first leg SEM. A. *P. lavatandroka*, patella, spur. D. claw tuft. E. claws, prolateral. B. *P. mazavaloha*, femur, scales. C. leg I, proventral. Scale bars for A = 0.5 mm, B = 100 µm, C = 1 mm, D = 30 µm, E = 100 µm.

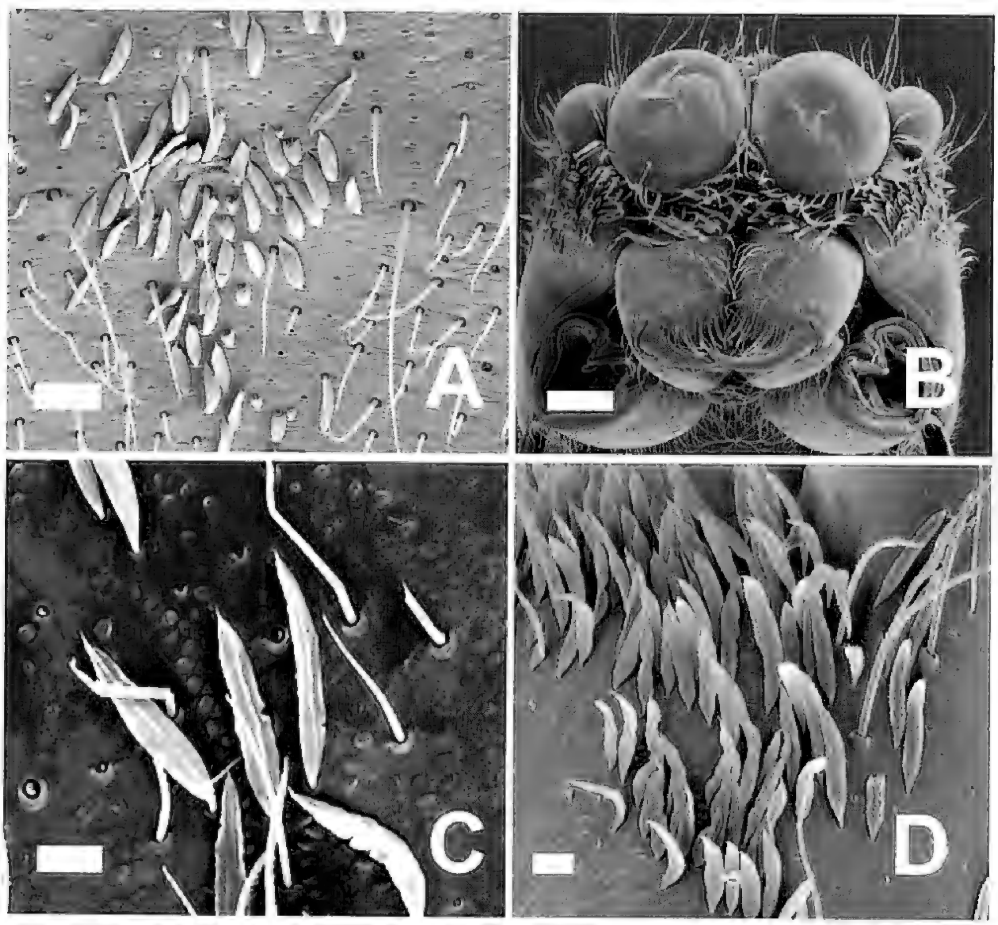


FIGURE 53 (above). *Padilla* carapace texture, scales. A. *P. mazavaloha*, carapace texture, scales. B. *P. lavatandroka*, female, carapace, front view showing scales above clypeus. C. *P.* lavatandroka, carapace texture, scales. D. scales around lateral eyes and on lateral margins of carapace. Scale bar for A = 20 µm, B = 200 µm, C = 10, D = 30µm.

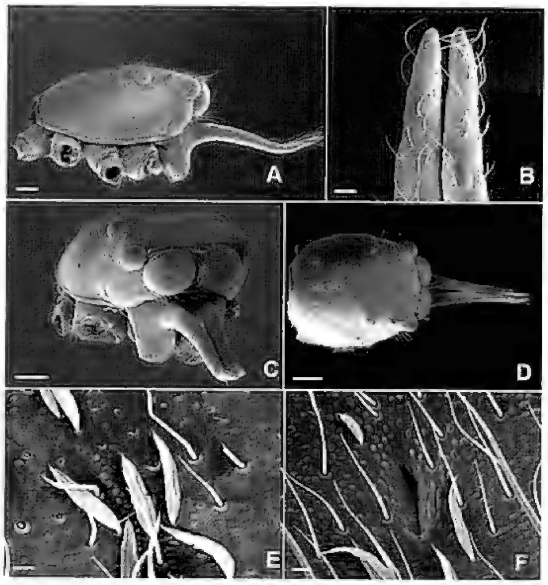
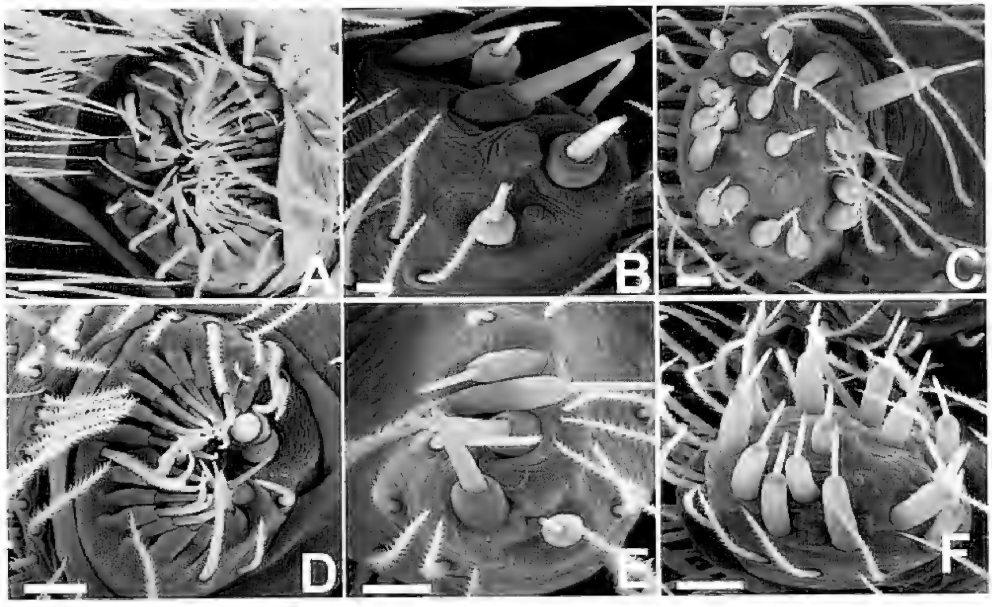
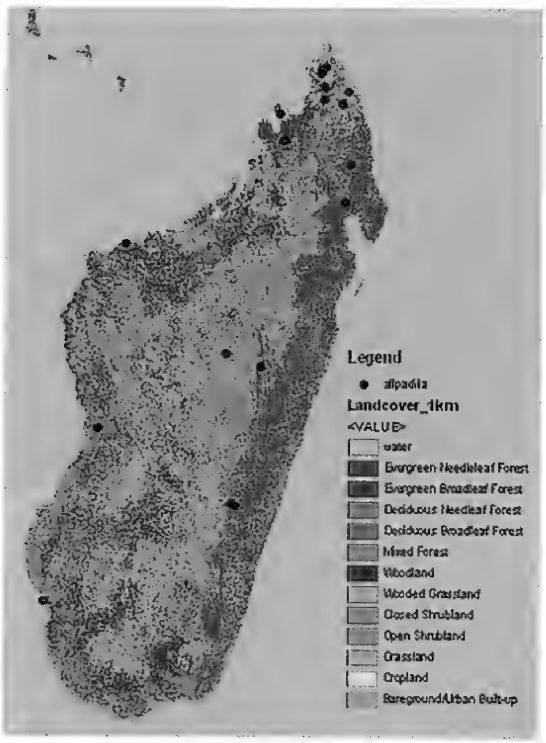


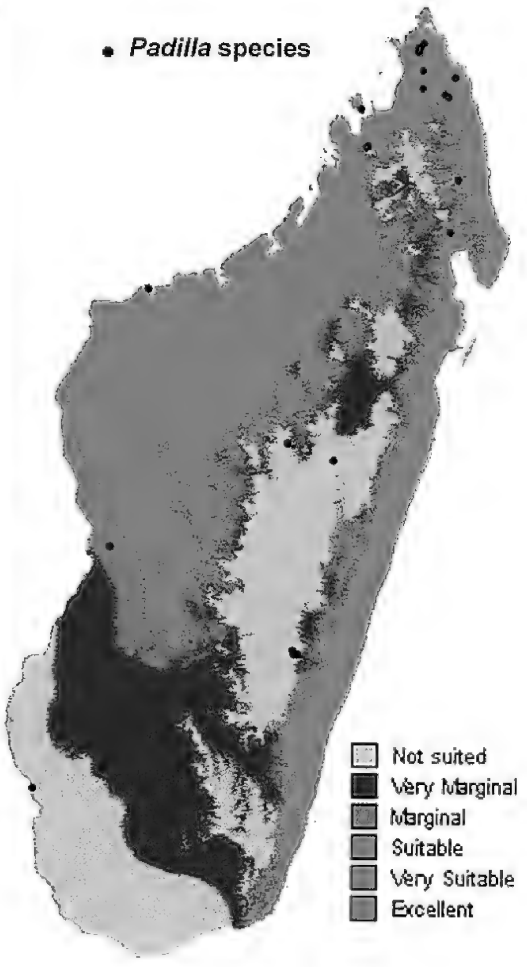
FIGURE 54 (right). *Padilla* horn, horn tips, carapace scales, fovea. A. *P. lavatandroka*, carapace, lateral. B. carapace, dorsal. C. carapace, front. D. Horn tips dorsal, showing hairs and stridulating files. E. carapace scales near fovea. F. fovea. Scale bars for A, B. C = 30µm, D = 20 µm, E, F = 10 µm .

FIGURE 55 (right). *P. boritandroka*, habitus, dorsal. Scale bar = 1 mm.

FIGURE 56 (below). *Padilla* spinning organs. *P. lavatandroka*: A. left ALS. B. left, PMS. C. right, PLS. *P. lavatandroka*: D. right ALS. E. left, PMS. F. right, PLS. Scale bars for all 20 µm.







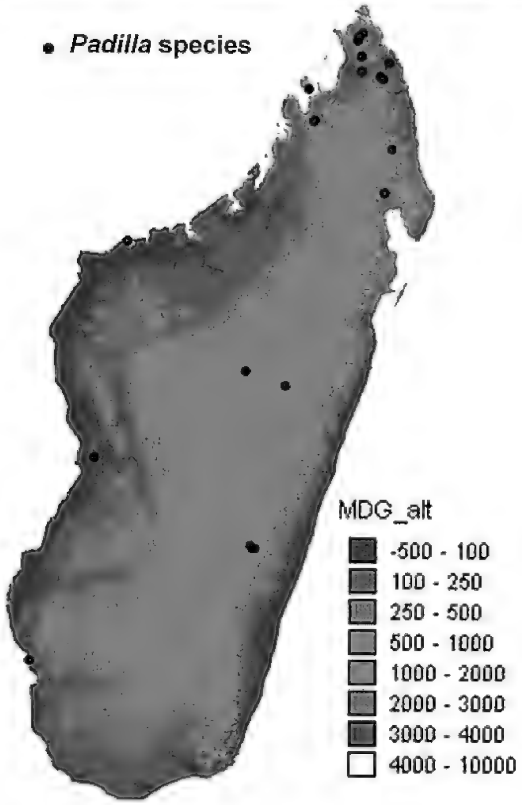


FIGURE 57 (upper left). Vegetation distribution map for all members of the genus *Padilla* in Madagascar.

FIGURE 58 (lower left). Altitudinal distribution map for *Padilla* species.

FIGURE 59 (upper right). Suitable area for the members of the genus *Padilla*.

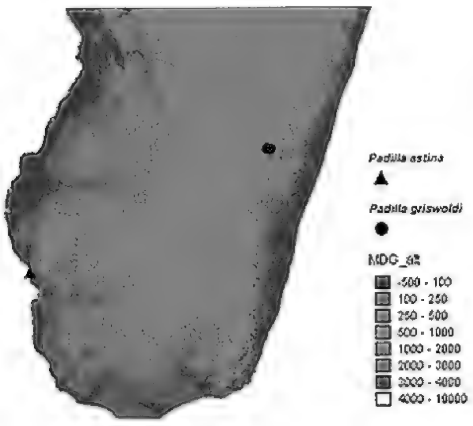


FIGURE 60. Altitudinal distribution map for *P. griswoldi* and *P. astina* clade.

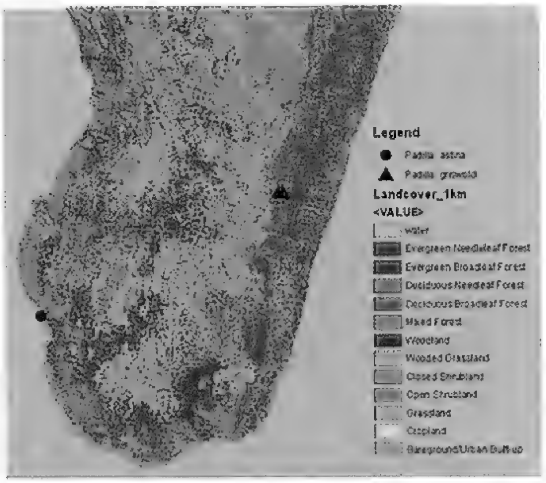
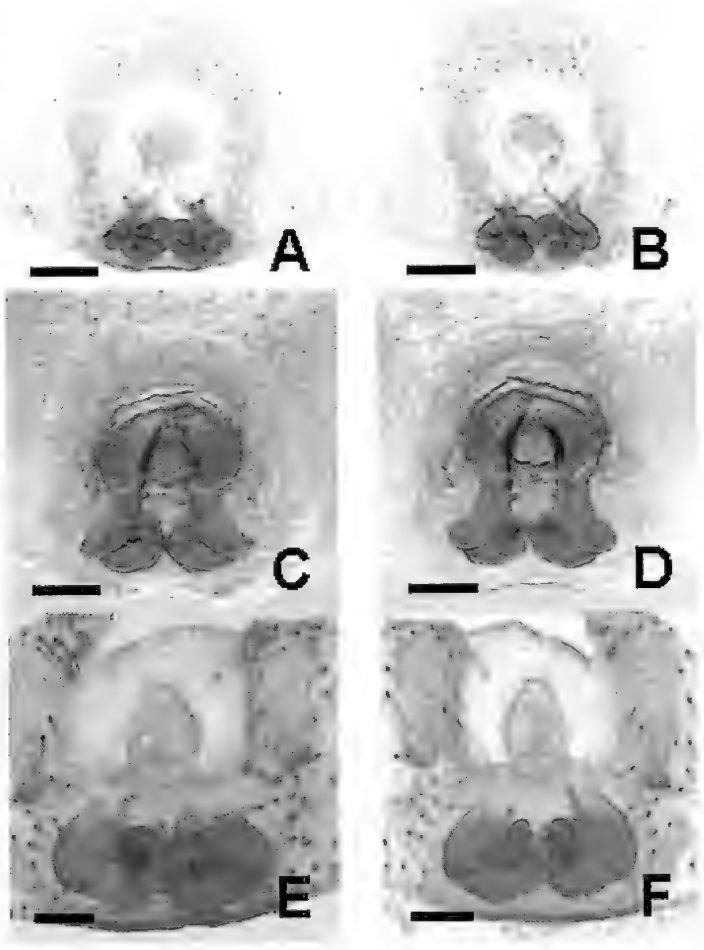


FIGURE 61. *P. griswoldi*, *P. astina* clade vegetation map.

FIGURE 62 (right). *Cornuta* group female epygina. A. *P. cornuta*, epyginum, ventral. B. epyginum, dorsal. C. *P. manjelatra*, epyginum, ventral. D. epyginum, dorsal. E. *P. lavatandroka*, epyginum, ventral. F. epyginum, dorsal. Scale bars for all = 0.2 mm.



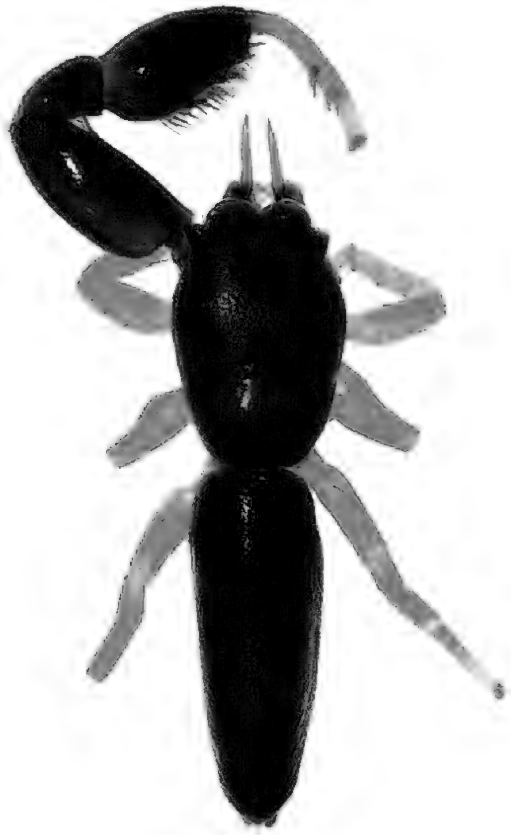


FIGURE 63. *P. ngeroka*, habitus, dorsal. Scale bar = 1 mm.

Appendix. 1. Species groups:

Armata group
- *P. armata* Peckham and Peckham, 1894
- P. ASTINA, new species
- *P. griswoldi*, new species
- *P. ombimanga*, new species

Brevis group
- *P. boritandroka*, new species
- *P. ngeroka*, new species

Cornuta group
- *P. cornuta* (Peckham and Peckham, 1885)

Discussion).
- *P. lavatandroka*, new species
- *P. manjelatra*, new species

Sartor group
- *P. maingoka*, new species
- *P. mazavaloha*, new species
- *P. sartor* Simon, 1900

Unassigned
- *P. foty*, new species
- *P. mihaingo*, new species
- *P. mitohy*, new species

Appendix 2. Anatomical and Institutional abbreviations

Abd L	abdomen length
AC	aciniform gland spigot
ALS	anterior lateral spinnerets
ALE-PME	distance between anterior lateral eyes and posterior median eyes
ap	additional promarginal spine
ar	additional retromarginal spine
CL	carapace length
cpltxL	cephalothorax length
CH	height cephalothorax
CHL	cheliceral length
co	copulatory openings
CW	chelicerae width
dAME	diameter of the anterior median eyes
DH	distal origin of the horns
ec	embolus coil
ef	embolus fold
el	embolus second loop
ek	transluscent septum
er	endite ridge
esl	embolar second loop
F1	femur I length
F3	femur III length
F4	femur IV length
fd	fertilization ducts
H clyp	height clypeus
HL	horn length
HL/ CL	horn length/ Carapace length
HW	horn width
HW/ HL	horn width/ Horn length
L.O.F	length Ocular Field
MAP	major Ampulate
mAP	minor Ampulate
MLE	maximum likelihood
Mt 1	metatarsus I length
Mt 3	metatarsus III length
Mt 4	metatarsus IV length

Institutional abbreviations

CAS	California Academy of Sciences, San Francisco, California
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

Appendix. 3. Distribution of characters for 16 taxa: 15 *Padilla* species and one outgroup taxon. Character states are scored 0 - 3, "?" for unknown, "_" for unapplicable. Outgroup taxa is bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ballus chalybeius	0	_	_	_	_	_	_	0	0	0	0	0	0	0	1	0	0	0	1
Philates thaleri	0	_	_	_	_	_	_	0	_	1	0	0	0	0	1	0	0	1	0
P. sartor	1	1	3	0	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1
P. mazavaloha	1	1	3	1	2	1	1	1	0	0	0	1	0	1	1	0	0	1	1
P. maingoka	1	1	3	1	0	0	1	1	0	1	0	1	1	0	1	0	0	1	1
P. cornuta	1	0	2	0	1	1	1	1	0	1	0	1	0	1	1	0	0	1	1
P. manjelatra	1	0	2	0	2	2	1	1	0	1	1	1	0	1	1	1	0	1	1
P. lavatandroka	1	0	2	0	2	2	1	1	0	1	1	1	0	1	1	1	0	1	1
P. mitohy	1	_	_	_	_	_	_	1	0	0	0	1	1	0	1	0	0	1	0
P. foty	1	_	_	_	_	_	_	1	0	1	0	1	0	0	1	0	0	0	1
P. mihaingo	1	_	_	_	_	_	_	1	0	0	0	1	1	0	1	0	0	1	0
P. armata	1	2	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	1
P. astina	1	2	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0
P. griswoldi	1	2	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1	1	0
P. ombimanga	1	2	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1	1
P. boritandroka	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	1	1
P. ngeroka	1	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0	1

	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Ballus chalybeius	2	2	1	1	0	1	1	0	0	0	1	1	1	1	1	0	0	1	0
Philates thaleri	1	1	1	1	1	0	0	0	0	0	0	1	1	1	0	0	0	1	1
P. sartor	1	1	1	1	1	1	1	0	0	2	1	0	1	1	1	0	0	_	0
P. mazavaloha	1	1	1	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0
P. maingoka	0	0	1	0	1	1	1	0	0	0	1	0	1	1	1	0	0	_	0
P. cornuta	1	1	1	0	1	1	1	0	0	0	1	1	1	1	1	2	0	1	0
P. manjelatra	2	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	0	0
P. lavatandroka	2	1	1	1	1	1	1	0	0	1	1	0	1	1	1	1	0	1	0
P. mitohy	0	0	0	0	1	1	1	0	0	0	1	0	_	_	_	_	_	1	1
P. foty	1	0	1	0	0	1	1	0	0	0	1	0	_	_	_	_	_	1	1
P. mihaingo	0	0	0	0	1	1	1	0	0	0	1	0	_	_	_	_	_	0	0
P. armata	1	1	0	1	1	1	1	0	0	0	1	0	1	1	1	2	1	_	0
P. astina	1	1	0	1	1	1	1	0	0	0	0	0	1	1	1	2	1	_	0
P. griswoldi	1	1	0	1	1	1	1	0	0	0	0	0	1	1	1	2	1	_	0
P. ombimanga	1	1	1	1	1	1	1	0	0	2	1	0	1	1	1	2	1	_	0
P. boritandroka	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	_	0
P. ngeroka	0	0	1	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0

Appendix. 4. Distribution of characters for 18 Ballinae species. This matrix is a reproduction of Benjamin (2004) ballinae matrix in which we added two *Padilla* species and two other characters that are judged to be synapomorphic to the genus. Character states are scored 0 - 2, "?" for unknown, "-" for unapplicable. Outgroup taxon is bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Baviola braueri	0	0	_	0	0	0	0	0	0	1	0	0	0	0	0	0	_	0	_	0	0
Cynapes wrighti	0	1	?	1	1	0	0	0	0	1	0	0	0	0	0	0	_	0	_	0	0
C. conosus	1	1	?	1	1	0	?	0	0	1	1	0	0	0	0	0	_	1	0	0	0
Colaxes wanlessi	1	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	_	1	0	1	0
Ballus chalybeius	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	0	_	1	2	1	1
B. segmentatus	1	1	0	1	1	0	1	0	0	1	1	0	0	0	0	0	_	1	0	1	1
Indomarengo sarawakensis	1	1	1	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	0	1	0
I. chandra	1	1	1	1	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	1	0
Leikung porosa	1	1	2	1	2	1	0	0	0	0	_	0	1	1	1	1	1	0	_	1	0
Afromarengo coriacea	1	1	1	1	2	1	0	0	0	0	_	0	1	0	1	1	1	0	_	1	0
Philates grammicus	1	1	?	1	1	2	?	0	0	1	1	1	0	0	0	1	1	1	0	1	0
P. zschokkei	1	1	1	1	1	2	1	1	0	1	1	0	0	0	0	1	1	1	0	1	0
Marengo crassipes	1	1	0	1	1	2	0	0	0	1	1	0	0	0	0	0	_	1	0	1	0
M. deelemanae	1	1	1	1	1	2	0	0	0	1	1	0	0	0	0	0	_	1	0	1	0
Philates chelifer	1	1	1	1	1	2	1	0	0	1	1	0	0	0	0	1	_	1	1	1	0
Sadies fulgida	1	1	2	1	1	2	0	0	0	1	1	0	0	0	1	1	0	0	_	1	0
Padilla manjelatra	1	1	2	1	1	1	1	0	1	1	1	0	0	0	0	1	1	0	1	0	0
Padilla mazavaloha	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	0

	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
Baviola braueri	0	0	0	0	0	0	0	0	0	0	0	0	_	1	1	0	0	0	0	0	0
Cynapes wrighti	0	0	0	1	0	1	0	0	1	0	0	0	_	1	0	1	0	0	0	0	0
C. conosus	0	0	0	0	0	1	0	0	1	0	0	0	_	1	0	1	0	0	1	0	0
Colaxes wanlessi	0	0	0	1	0	0	0	0	1	1	0	0	_	0	1	0	0	0	0	0	0
Ballus chalybeius	0	0	0	0	0	1	0	0	1	1	0	0	_	0	1	0	0	0	0	0	0
B. segmentatus	0	0	0	0	1	1	0	0	1	0	0	0	_	0	1	0	0	0	0	0	0
Indomarengo sarawakensis	0	0	1	0	0	1	1	0	1	1	0	1	2	1	0	0	0	0	0	0	0
I. chandra	0	0	1	0	0	1	1	0	1	1	0	1	2	1	1	?	0	1	0	0	0
Leikung porosa	0	0	1	0	0	1	1	1	1	1	0	1	2	2	0	0	1	1	0	0	0
Afromarengo coriacea	1	0	1	0	0	1	1	0	1	1	1	1	1	1	0	0	0	1	0	0	0
Philates grammicus	1	0	0	0	0	1	0	0	1	1	0	1	?	1	?	?	0	0	0	0	0
P. zschokkei	1	0	1	0	0	1	0	0	1	1	0	1	0	1	?	?	0	0	0	0	0
Marengo crassipes	1	1	0	0	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0	1	0
M. deelemanae	1	1	0	0	0	1	0	0	1	1	0	1	0	1	?	?	0	0	0	1	0
Philates chelifer	0	1	0	0	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0
Sadies fulgida	1	0	1	0	0	1	1	0	1	0	0	0	_	1	0	1	0	0	0	0	0
Padilla manjelatra	1	0	0	0	1	1	0	1	1	1	0	0	_	1	0	1	0	0	0	1	1
Padilla mazavaloha	1	0	0	0	0	0	0	0	1	1	0	0	_	1	0	1	0	0	0	1	1

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Studies of the Subtribe Tachyina (Coleoptera: Carabidae: Bembidiini)

Supplement E: A Revision of the Genus *Costitachys* Erwin 1974

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The Neotropical genus *Costitachys* Erwin 1974 is revised. Newly discovered specimens of a new species of *Costitachys* from Ecuador provide comparative genitalic characters of males for the genus and extend its range 2900 km west of its previously known distribution into an additional center of species radiation in South America, the "North Andean Slope." A new species, *Costitachys tena* Erwin and Kavanaugh sp. nov. (type locality: Ecuador, Napo Province, Tena, 598 m, 0°59′S, 077°49′W) is described. One additional locality for *Costitachys inusitatus* Erwin is recorded from Brazil and another noted from French Guyana. A key to facilitate identification of adults of the two species is included.

KEYWORDS: Brazil, Ecuador, French Guyana, Perú, Trinidad, Carabidae, Bembidiini, Tachyina, *Costitachys* Erwin.

Resumen

El género Neotropical *Costitachys* Erwin 1974 es revisado. El descubrimiento de especímenes de una nueva especie de *Costitachys* provenientes de Ecuador proporcionaron caracteres comparativos de la genitalia de los machos para este género y extendió su rango de distribución 2,900 km al oeste de la distribución previamente conocida, dentro de un centro de radiación de especies adicional en Sudamérica, la "Pendiente Andina del Norte." Una nueva especie, *Costitachys tena* Erwin and Kavanaugh sp. nov. (Localidad tipo: Ecuador, Provincia de Napo, Tena, 598 m, 0°59′S, 077°49′W) es descrita. Una nueva localidad para *Costitachys inusitatus* Erwin se agrega para Brasil y otra para Guayana Francesa. Se incluye una clave para facilitar la identificación de los adultos de ambas especies.

PALABRAS CLAVAE: Brasil, Ecuador, Guayana Francesa, Perú, Trinidad, Carabidae, Bembidiini, Tachyina, *Costitachys* Erwin.

Costitachys inusitatus Erwin was described (Erwin 1974b) on the basis of a single female from Santarém, Pará, Brazil. This beetle's distinctive form (Fig. 1), striking among Tachyina worldwide, warranted its description as both a new species and new genus even though only a single specimen was known. Two additional specimens were found subsequently among unsorted carabid beetles at the California Academy of Sciences (CAS) and Museu Goeldi (MGBB) (one female and one male, respectively); and updated information about the genus, including description and illustration of the unusual male genitalia, was provided by Erwin and Kavanaugh (1999).

Recently, we discovered an additional specimen of *C. inusitatus* among specimens borrowed from the collection of Museu Goeldi as well as another 11 specimens among unsorted materials in the National Museum of Natural History (NMNH). The latter are undoubtedly members of *Costitachys* but represent an undescribed species from the western side of the Amazon Basin in Ecuador and Perú. The purpose of this paper is to present new information, compare and contrast the two known species, and provide hypotheses regarding their way of life and trans-Amazon distribution.

Methods

Measurements recorded here include ABL (apparent body length = distance along midline from apex of labrum to apex of longer elytron); SBL (standardized body length = the sum of the lengths of the head [measured from apex of clypeus to a point on midline at level of posterior margin of compound eye], pronotum [measured from apical margin to basal margin along midline], and elytra [measured along midline from apex of scutellum to apex of the longer elytron]); and TW (total width = width across both elytra at their widest point). The code for elytral chaetotaxy is as proposed by Erwin (1974a).

Male specimens were dissected as previously described by Erwin and Kavanaugh (1981) and Kavanaugh (1979). We did not dissect and examine female reproductive tract structures for two reasons. First, because of the small size of these beetles and the extreme difficulty associated with safe dissection of these delicate structures, the likelihood of causing irreparable damage during dissection is high. Second, little or no comparative data exist for characters of the female reproductive tract in other tachyine taxa. We chose not to risk destroying reproductive tract structures in these few important *Costitachys* specimens at a time when the dissections, even if successfully done, would have little comparative value. Study of the female tract of these specimens should await the development of a body of comparative data based on dissections of specimens of more abundant and easily obtained tachyine species.

Illustrations of the male aedeagal median lobe and parameres were made using a camera lucida mounted on a Wild compound microscope. Digital images of habitus were taken using an Automontage imaging system by Syncroscopy® with a Leica M420 dissecting microscope.

Costitachys Erwin, 1974

Costitachys Erwin, 1974:128. Type species: *C. inusitatus* Erwin, 1974, by monotypy.

Derivation of name.— Latin, *costa,* meaning rib and referring to the longitudinal carinae of the head, pronotum, and elytra; plus *Tachys,* the nominate genus of the subtribe, hence the Tachyina with ribs.

Diagnosis.— Broad and subdepressed, easily distinguished from other Tachyina by the multiple carinae of the head, pronotum, and elytra. In addition, adults have only one pair of supraorbital setae, a feature found elsewhere among tachyines only in genus *Micratopus* Casey, all known members of which are non-carinate.

Description.— Size moderately small for subtribe: ABL males = 1.7 to 2.3, females = 1.9 to 2.6 mm; SBL males = 1.5 to 2.3 mm, females = 1.9 to 2.4 mm; TW males = 0.8 to 1.0 mm, females = 0.9 to 1.2 mm *Color:* flavotestaceous throughout or elytron with darker discal cloud; antennae testaceous. *Luster:* surface shiny. *Head:* clypeus and dorsum of head with three longitudinally oriented carinae; one supra-orbital seta per eye; eyes micro-setiferous; mentum without foveae, with minute tooth along anterior margin; antennae short, extended to base of prothorax, and antennomeres 2–11 pubescent. *Prothorax:* pronotum with five longitudinally oriented carinae; without

setae at base or along lateral margin. *Pterothorax:* elytra impunctate; with eight longitudinally oriented carinae, sixth continuous with rounded humeral margin; marginal explanation nonsetose, nonserrate; recurrent groove absent; chaetotaxy formula Eo 1a, 2a, 3a, 4a, 5c, 6b, 7, 8a; Ed 1, 7b. *Legs:* anterior tibia markedly obliquely notched apicolaterally; males with basitarsomere (tarsomere 1) on anterior tarsi expanded, about 1.5 times wider than tarsomere 4, medially dentiform, and with a small pad of adhesive setae ventrally (anterior tarsomere 1 more slender, edentate, and without pad of adhesive setae ventrally in females); otherwise, legs normal for Tachyina. *Abdomen:* last visible sternite of male and female each with one pair of ambulatory setigerous pores, females with very short pubescence either broadly and sparsely distributed over sternite or confined to a small patch located medially on the sternite between the two "ambulatory" setae, males with or without broadly and sparsely distributed pubescence.

GEOGRAPHIC DISTRIBUTION.— Widespread in the eastern Amazon Basin, north to French Guyana and Trinidad, west to the eastern Andean slopes of Ecuador and Perú.

Checklist of Species of *Costitachys* Erwin

Costitachys inusitatus Erwin. Brazil, French Guyana, Trinidad
Costitachys tena Erwin and Kavanaugh, sp. nov. Ecuador, Perú

Key to Species of *Costitachys* Erwin

1 Pronotum with side margins rounded (Fig. 1). . . . . *C. inusitatus* Erwin
1' Pronotum with side margins sinuate posteriorly (Fig. 2). . *C. tena* Erwin and Kavanaugh, sp. nov.

Costitachys inusitatus Erwin

Figures 1, 3, and 5.

TYPE.— HOLOTYPE, a female (deposited in Museum of Comparative Zoology, Harvard University), Santarém, Pará, Brazil.

DERIVATION OF NAME.— Latin, *inusitatus,* meaning unusual and referring to the bizarre structure of the dorsal surface of these beetles in relation to other Tachyina.

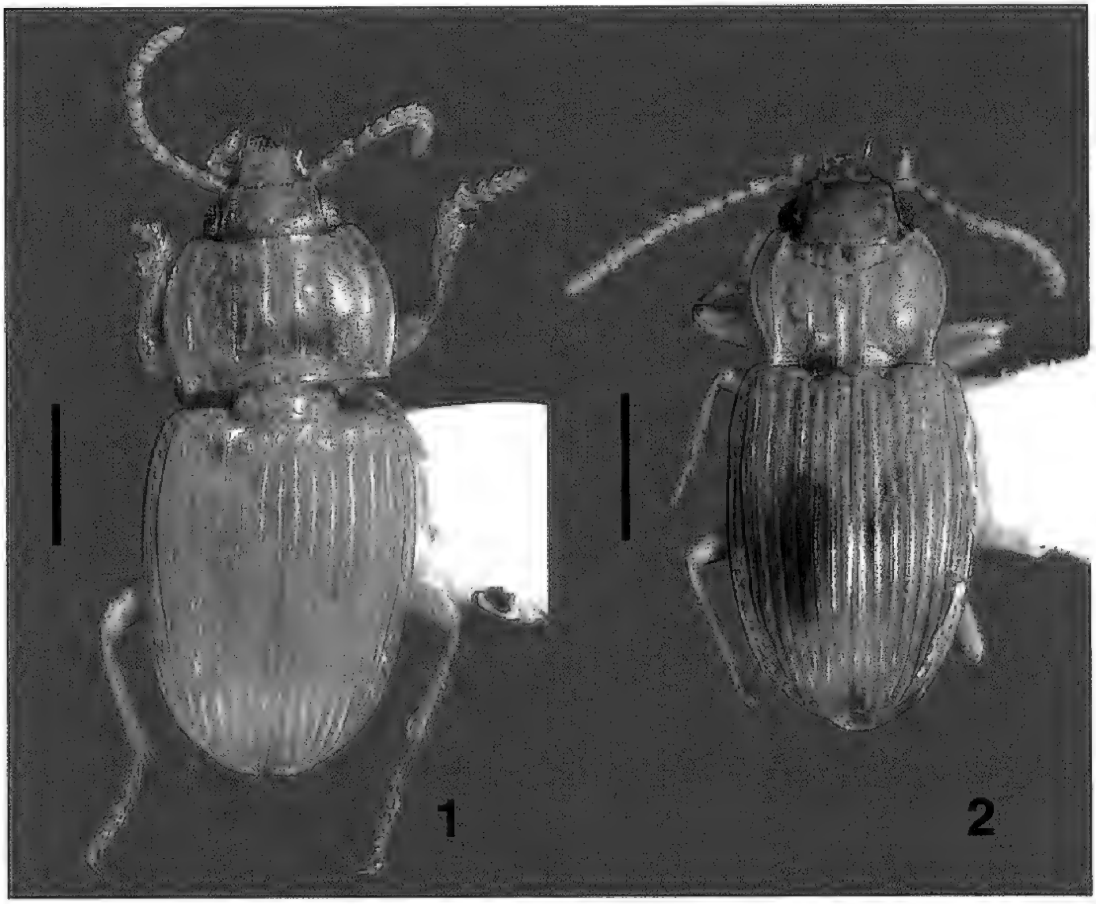
COMMON NAME.— Unusual ribbed rapid carabid.

DIAGNOSIS.— Pronotum with side margins rounded, hind angles obtuse; central disc of elytron without diffuse darker cloud; female with pubescence on last visible sternite confined to a small patch medially between the two "ambulatory" setae, male without pubescence; male with left paramere of aedeagus broad, conchoid, truncate apically, with four or five lanceolate apical setae (Fig. 3b).

DESCRIPTION.— With the attributes listed above in the genus description; size large for genus: ABL males = 2.3 mm, females = 2.3 to 2.6 mm; SBL males = 2.2 mm, females = 2.2 to 2.4 mm; TW males = 1.0 mm, females = 1.0 to 1.2 mm. *Color:* flavotestaceous throughout, antennomeres paler. *Prothorax:* pronotum with side margins rounded, hind angles obtuse. *Male:* median lobe of aedeagus (Fig. 3a) with apex broadly rounded; left paramere (Fig. 3b) conchoid, truncate apically, with four or five long and lanceolate apical setae; right paramere short and slender with four very long, slender apical setae.

SPECIMENS EXAMINED.— A total of four specimens (2 males and 2 females) from the following localities: BRAZIL: Pará, Salinas [6 January 1962; J. & B. Bechyné collectors] (1 male; MGBB), Santa Isabel [6 June 1962; J. & B. Bechyné collectors] (1 male ; MGBB), Santarém [April 1963, F.G. Werner collector] (1 female; MGBB). TRINIDAD: Cocos Bay [1 February 1969; L. & C.W. O'Brien collectors] (1 female; CAS).

The male specimen from Salinas (probably at 1°17′49″S, 47°55′06″W, 37 m), Pará, Brazil, collected by



FIGURES 1–2. Digital images of habitus, dorsal aspect.; scale lines = 0.5 mm. 1. *Costitachys inusitatus* Erwin; 2. *Costitachys tena* Erwin and Kavanaugh, sp. nov.

J. & B. Bechyné (Museu Goeldi) (ADP103054), is here reported for the first time. Unfortunately, there are several "Salinas" east of Belém, Brazil, in the area where the Bechynés worked during the early 1960s. However, the site cannot be far from Santa Isabel (probably at 1°17′34″S, 48°08′57″W, 20 m) because the two specimens from "Salinas" and Santa Isabel were collected on the same day.

NOTES.— When we described the male genitalia of *C. inusitatus* (Erwin and Kavanaugh 1999), we had overlooked a previous description by Perrault (1984) in a "Scientific Note" based on a specimen from French Guyana. We have not yet had an opportunity to examine that specimen, which Perrault recorded as slightly smaller (2.2 mm) than specimens we have examined, but our illustration of the genitalia of the male from Santa Isabel, Brazil agrees in detail with that Perrault's of the French Guyanan specimen, except that the latter appears (in Perrault's Fig. 1a) to have four apical setae, rather than five as we illustrated (our Fig. 1).

HABITAT DISTRIBUTION.— Perrault (1984) reported that his specimen, collected by N. Dagallier (ORSTOM), was found "by sifting sand on Montjoly Beach near Cayenne". This is solid evidence that this species is riparian, occurring on light colored sandy river margins.

***Costitachys tena* Erwin and Kavanaugh, sp. nov**

Figures 2, 4, and 5.

Types.— Holotype, a female (deposited in NMNH), labeled: "Ecuador: Napo Tena 26 May 1977, W.E. Steiner"/ [♀]/ "ADP 103048"/ "HOLOTYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [red label]. A total of 10 paratypes (6 males and 4 females): 1 male (NMNH), labeled: "Ecuador: Napo Tena 26 May 1977, W.E. Steiner"/ [♂]/ "ADP 103056"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 1 male (NMNH) labelled: "Ecuador, Post. Tena (3 km N) Blacklight 5 July 1976 Jeffrey Cohen"/ "Ecuador – Peace Corps – Smithsonian Institution Aquatic Insect Survey"/ [♂]/ "ADP 103050"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 1 male (NMNH) labeled: "Ecuador, Post. Tena (3 km N) Blacklight 5 July 1976 Jeffrey Cohen"/ "Ecuador – Peace Corps – Smithsonian Institution Aquatic Insect Survey"/ [♂]/ "ADP 103052"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 1 male (CAS), labeled: "Ecuador, Post. Tena (3 km. N) Blacklight 5 July 1976 Jeffrey Cohen"/ "Ecuador – Peace Corps – Smithsonian Institution Aquatic Insect Survey"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 2 females (1 in CAS, 1 in NMNH), labeled: "Ecuador: Napo Puerto Nuevo (2 km S) 9 July 1976 Jeffrey Cohen"/ "collected at black light"/ "Ecuador – Peace Corps – Smithsonian Institution Aquatic Insect Survey"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 1 female (NMNH), labeled: "Ecuador: Napo; Puerto Nuevo 8 July 1976 at blacklight J. Cohen"/ "Ecuador – Peace Corps – Smithsonian Institution Aquatic Insect Survey"/ "ADP 103058"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 1 female (NMNH), labeled: "Ecuador: Napo; Puerto Nuevo 8 July 1976 at blacklight J. Cohen"/ "Ecuador – Peace Corps – Smithsonian Institution Aquatic Insect Survey"/ [ADP 103060"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 1 male (NMNH), labeled: "Ecuador: Napo; Puerto Nuevo 8 July 1976 at blacklight J. Cohen"/ "Ecuador – Peace Corps – Smithsonian Institution Aquatic Insect Survey"/ "ADP 103072"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label]; 1 male (NMNH), labeled "PERU, Guanaco, Penguin Biological Station, Rio Yuyapichis, 9°37′S, 74°56′W, W. Hanagarth collector"/ "RB248 Bem XVa"/ "PARATYPE *Costitachys tena* n. sp. designated by T.L. Erwin & D.H. Kavanaugh 2007" [yellow label].

Derivation of name.— Tena is the name of a town, which is near the type locality and is used as a noun in apposition.

Common name.— Tena ribbed rapid carabid.

Diagnosis.— Pronotum cordiform with lateral margins sinuate posteriorly; head (Fig. 2) markedly wider in relation to the width of the pronotum; central disc of elytra with a diffuse slightly darker cloud; both male and female with broadly and sparsely distributed pubescence on last visible sternite; left paramere of male aedeagus long and slender, with three long and slender apical setae (Fig. 4b).

Members of this species are easily distinguished from those of *C. inusitatus* by their cordiform pronota with lateral margins distinctly sinuate posteriorly (pronota not cordiform and lateral margins arcuate throughout their length in *C. inusitatus* adults [Fig. 1]) and heads that are wide in relation to pronotal width (head relatively narrower in *C. inusitatus* adults).

Description.— With the attributes listed above under the genus description; size small for genus: ABL males = 1.7 to 2.0 mm, females = 1.9 to 2.1 mm; SBL males = 1.5 to 1.8 mm, females = 1.9 to 2.0 mm; TW males = 0.8 to 0.9 mm, females = 0.9 to 1.0 mm. *Color:* flavotestaceous, disc of elytra with a dark cloud, antennomeres testaceous. *Prothorax:* pronotum with side margins sinuate basally, hind angles approximately rectangular. *Male:* median lobe of aedeagus (Fig. 4a) with apex narrowly produced; left paramere (Fig. 4b) long and slender, with three long and slender apical setae; right paramere short and slender with three medium-length apical setae.

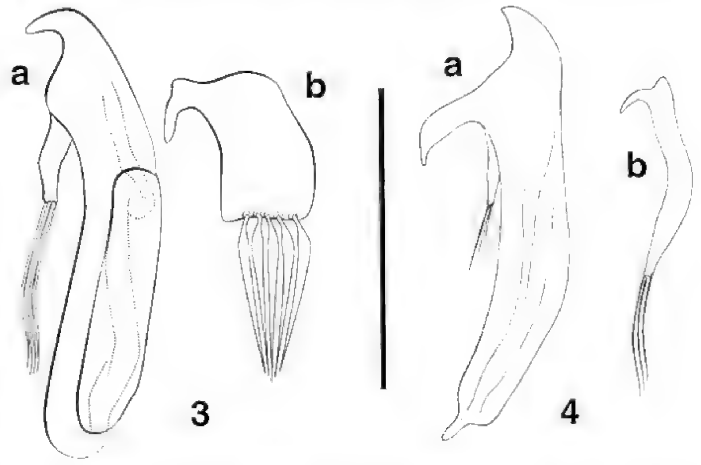
Specimens examined.— The type series of 11 specimens is listed above.

HABITAT DISTRIBUTION.— All the Ecuadorian specimens representing this new species were collected at a blacklight set up on the graveled shore of a small tributary of the Napo River at Tena, also near Tena, and at "Puerto Nuevo", now named Puerto Napo. This is good evidence that this species is riparian, occurring on graveled and/or sandy river margins.

DISCUSSION

Morphological Considerations

Two of the most intriguing morphological features of *Costitachys inusitatus* males are the shapes of the left paramere of the aedeagus and of the apical setae found on that structure. The conchoid form and broadly truncate apex of the paramere and its long and flattened lanceolate apical setae (Fig. 3b) are highly distinctive features among tachyine carabids. When we found and described these features (Erwin and Kavanaugh 1999), we assumed that they would prove to be good characters (i.e., synapomorphies) not just for *C. inusitatus* males, but also for males of any and all other species of *Costitachys* that might be discovered subsequently (i.e., that they would represent synapomorphies at a higher taxonomic level). So we were surprised to find in the second species, *C. tena*, described here, forms of the left paramere and of its apical setae (Fig. 4b) more typical of tachyines in general than of *C. inusitatus* males. This was all the more surprising given the obvious synapomorphies of external form and structure (e.g., the distinctive carinae of the head, pronotum, and elytra found nowhere else among tachyines) uniting these two species. We have no idea what differences in function or evolutionary significance there may be to this divergence between *Costitachys* species, but it may also be reflected in the differences between the pubescence patterns on the last visible sternite of the two species. In both males and females of *C. tena*, there is similar sparse, very short pubescence broadly distributed over the sternite; but in *C. inusitatus*, males have no pubescence on this sternite and females have the pubescence denser and restricted to a patch on the medial area between the apical paramedial "ambulatory" setae. This is probably an area on the female that comes in contact with the left paramere of the male during copulation; so it may be that the differences in features of the left paramere and of the last visible sternite are somehow correlated and coevolved.



FIGURES 3–4. Male genitalia, left lateral aspect; a = median lobe with right paramere attached; b = left paramere (detached); scale line = 0.25 mm. 3. *Costitachys inusitatus* Erwin; 4. *Costitachys tena* Erwin and Kavanaugh sp. nov.

Zoogeographical Considerations

Discovery of *C. inusitatus* Erwin in Cocos Bay, Trinidad, extended the range of that species north of its originally known type locality by 1550 km (Erwin and Kavanaugh 1999). The discovery of a second species of *Costitachys* in the cis-Andean region of Ecuador and Perú extends the

known range of the genus to the west some 2900 km (Fig. 5). The genus now has been recorded from three "centers of species radiation" in the Neotropics — namely, the "North Atlantic Coast," the "Lower Amazon — Mid-Atlantic Coast," and the "North Andean Slope" (see Erwin and Pogue 1988 for named centers). The western Amazonian species has been recorded along the margins of the Rio Napo (in Ecuador) and Rio Yuyapichis (in Perú); thus it is likely that members of this genus will be found throughout the Amazon Basin because they live along first-order rivers in the Amazon watershed. It is also likely that additional undescribed species await discovery. The margins of large Amazon Basin rivers have various types of microhabitats including both broad sand bars and cuts into forests resulting in steep banks of dark soil and roots. The pale color of adults of both *C. inusitatus* and *C. tena* suggests that these beetles probably occur on light-colored sandy alluvium, and this microhabitat is distributed throughout the Amazon drainage basin. The upper Napo River also has sand with an over-layer of small stones and gravel interspersed with exposed light-colored sand. Additional evidence for light-colored sand habitat comes from the specimen noted by Perrault (1984) collected on the beach at Montjoly in Cayenne, French Guyana. All of these habitats should be explored to discover more about these unusual Tachyina.

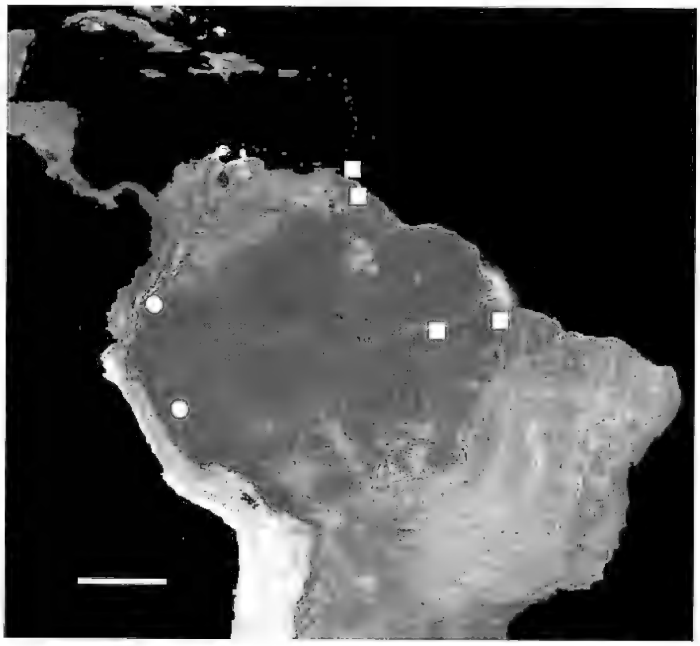


FIGURE 5. Map illustrating the geographical locations of known samples of *Costitachys inusitatus* Erwin (white squares) and *Costitachys tena* Erwin and Kavanaugh sp. nov. (white dots); scale line = 1000 km; map produced with NASA's World Wind.

ACKNOWLEDGEMENTS

We thank William Overal, curator at MGBB, for the loan of the male specimen from that institution and Wendy Moore (CAS) for her review of our manuscript. George Venable and Vichai Malikul (NMNH) provided the male illustrations, and Valeria Aschero provided the Spanish translation of the abstract.

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New Species of the Pennatulacean Genera *Acanthoptilum* and *Stylatula* (Octocorallia: Virgulariidae) from New Zealand and the Campbell Plateau: Both Genera Previously Considered Endemic to the West Coast of the Americas and Atlantic Ocean

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The pennatulacean genera *Renilla*, *Ptilosarcus*, *Stylatula*, and *Acanthoptilum* have formerly been treated as taxa endemic or restricted to particular regions of North and South America and parts of the Atlantic. Undescribed species of two of these genera (*Stylatula* and *Acanthoptilum*) have been collected from the region of New Zealand in the southwestern Pacific. The present paper reports this discovery and provides descriptions of these two new species.

Four genera of pennatulacean octocorals (*Renilla* – Renillidae; *Stylatula* and *Acanthoptioum* – Virgulariidae; and *Ptilosarcus* – Pennatulidae) have previously been recorded as geographically restricted to the Pacific Coast of the Americas and the Atlantic Ocean (Kükenthal 1915; Williams 1995; Zamponi and Pérez 1995; López-González et al. 2001; Castro and Medeiros 2001). In the past half century, two of these genera (*Stylatula* and *Acanthoptilum*) have been collected off New Zealand (from both the North and South Islands, as well as the Campbell Plateau), in the southwestern Pacific. One new species of each of these genera is described here, thereby extending the range of *Stylatula* and *Acanthoptilum* to the southwestern Pacific Ocean.

Material and Methods

Material representing a broad spectrum of pennatulacean taxa was collected during survey cruises (1959–1962) of the NZOI – New Zealand Oceanographic Institute, Wellington (now known as NIWA – National Institute of Water and Atmospheric Research), or NMNZ – National Museum of New Zealand. All material was fixed and preserved in 40% isopropyl alcohol or 75% ethanol. One other abbreviation appearing in the text is CAS – California Academy of Sciences.

Systematic Account

Family Virgulariidae Verrill, 1868

Five genera of circumglobal distribution — in subarctic, temperate, and tropical latitudes, 0–1100 meters in depth.

Genus *Acanthoptilum* Kölliker, 1870

Acanthoptilum Kölliker, 1870:569. Balss, 1910:41. Kükenthal, 1915:63. Bayer, 1957:382. Williams, 1995: 123.

DISTRIBUTION.— California, Gulf of Mexico, Lesser Antilles, New Zealand region (Fig. 6).

Acanthoptilum longifolium Williams, sp. nov.

Figures 1, 2, 3A–C, 6.

MATERIAL EXAMINED.— HOLOTYPE: CAS 173205, Sta. No. NIWA (NZOI) Z8440: New Zealand, Head of Dusky Sound, Fiordland, 30 m depth, 5 January 1988, coll. Chris Glasson; one specimen in three pieces. PARATYPE: CAS 173206, Sta. No. NIWA (NZOI) Z8440: same data as holotype; one entire specimen. OTHER MATERIAL: CAS 173207, Sta. No. NIWA (NZOI) J965: Campbell Plateau (50.80°S, 173°36.70′E), 118 m depth, 20 June 1981, coll. NIWA; one specimen in two pieces. CAS 173208, Sta. No. NIWA (NZOI) S371: Campbell Plateau (56.40°S, 170°01.40′E), 200 m depth, 28 January 1983, coll. NIWA; five specimens total: one entire specimen, three specimens in several pieces each, and one partial specimen.

DESCRIPTION OF THE HOLOTYPE.— The entire length of the holotype is 450 mm total length, 275 mm of which is rachis. The total length of the peduncle is 175 mm, which is in two parts (Fig. 1A). The axis is present throughout the entire length of the specimen, < 1.5 mm in diameter; lustrous white in color; generally cylindrical in cross section, but may have three rounded corners in the region of the peduncle. Polyp leaves are sickle-shaped, alternately disposed along rachis, up to 18 mm in length and 4 mm in width. The bases of the polyp leaves are without armature (irregular clusters of sclerites), although scattered sclerites are found in the polyp leaves, including the basal regions. Autozooids number 9–13 per leaf, often bulbous in the basal or central portions, approximately 1.5–2.0 mm in length. Tentacles have up to 12 pinnules per lateral side. Calicular teeth of the autozooids are mostly indistinct, ca. 3–6 in number, approximately 0.2–0.4 mm in length. Some of these are composed of a single vertical needle-like sclerite, whereas others form an inverted "V" of two converging sclerites. Siphonozooids are 4–6 in number, in short rows. Individual siphonozooids are approximately 0.2–0.5 mm in height. These are mostly low and rounded in shape, but some are conical with converging sclerites forming a pointed apex. The siphonozooids form short rows parallel to the width of the polyp leaves, which are located on the rachis adjacent to bases of polyp leaves (under the insertion of the leaves). Polyp leaves are relatively transparent, revealing numerous white ova (each approximately 0.2–0.3 mm in diameter), which are clearly visible in the gastric cavities (Fig. 1C). Sclerites are three-flanged needles scattered in the coenenchyme, polyp leaves, and polyps, 0.12–0.70 mm in length. Color of the wet-preserved holotype is cream-white throughout.

DISTRIBUTION.— Southwestern part of the South Island of New Zealand, and Campbell Plateau; 30–200 m in depth (Fig. 6).

ETYMOLOGY.— The specific epithet is derived from the Latin *longus* (long) and *folium* (a leaf), in reference to the relatively elongated polyp leaves of this species.

REMARKS.— Morphologically, species of the genus *Acanthoptilum* can be confused with those of the virgulariid genus *Scytalium*, as the two genera are superficially similar. However, the genus *Scytalium* is characterized by having only oval-shaped plates (that are not three-flanged) in the polyp leaves as well as other parts of the colonies, whereas *Acanthoptilum* has sclerites that are three-flanged spindles, sometimes with small ovals or rods as well (Williams 1995:123–124).

Kükenthal (1915:63–65) reports that the six previously described species of *Acanthoptilum* have 4–9 polyps per leaf. In contrast, *Acanthoptilum longifolium* sp. nov. has 9–13 polyps per leaf (Fig. 1B–C, 2B). Of the six previously described species, four are known from California (*Acan-*

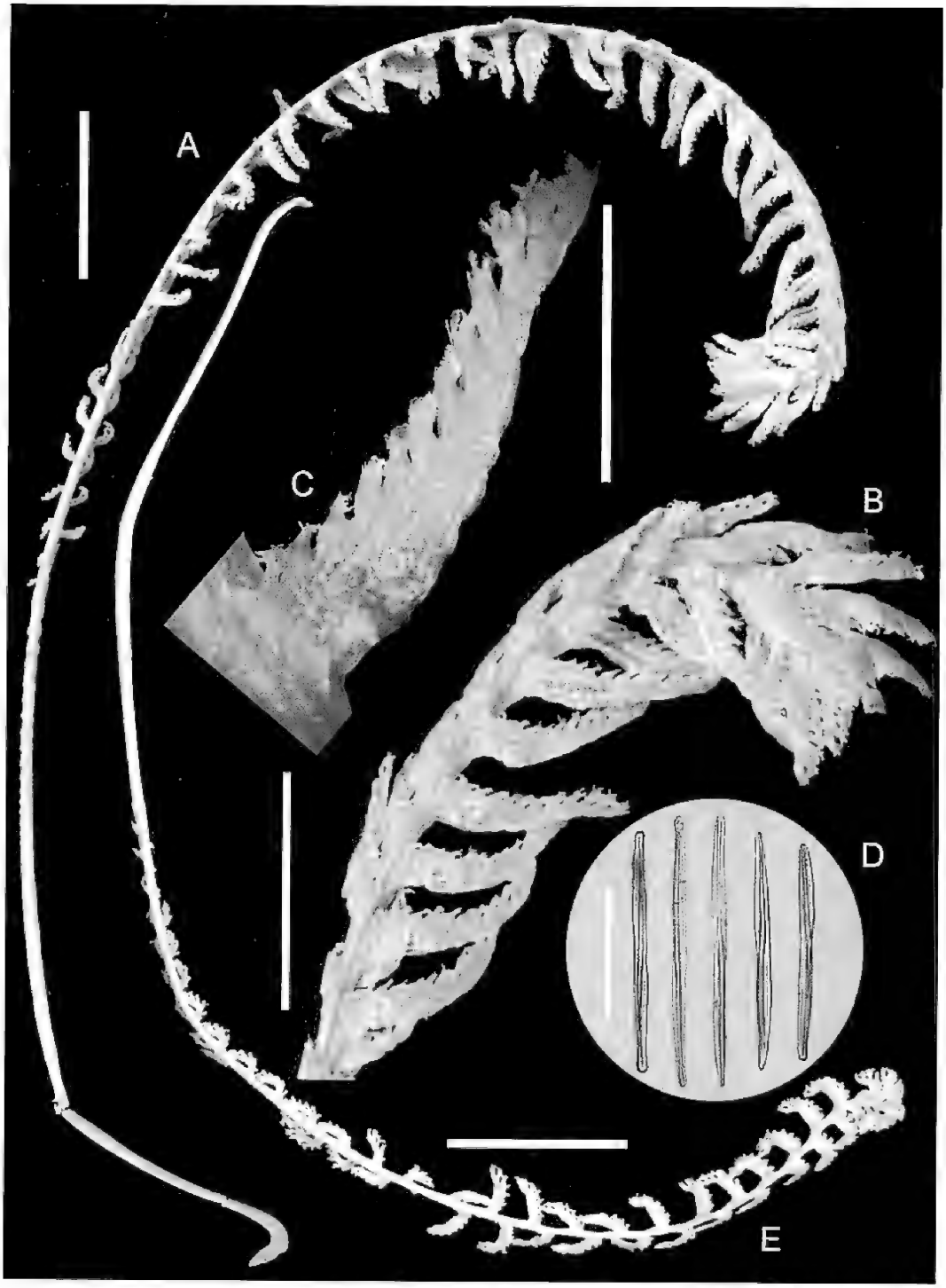

FIGURE 1. *Acanthoptilum longifolium* sp. nov. A-D. Holotype. A. Entire colony; scale bar = 30 mm. B. Distal end of rachis; scale bar = 20 mm. C. A single polyp leaf; scale bar = 8.0 mm. D. Five sclerites from a polyp leaf; scale bar = 0.3 mm. E. Paratype; scale bar = 30 mm.

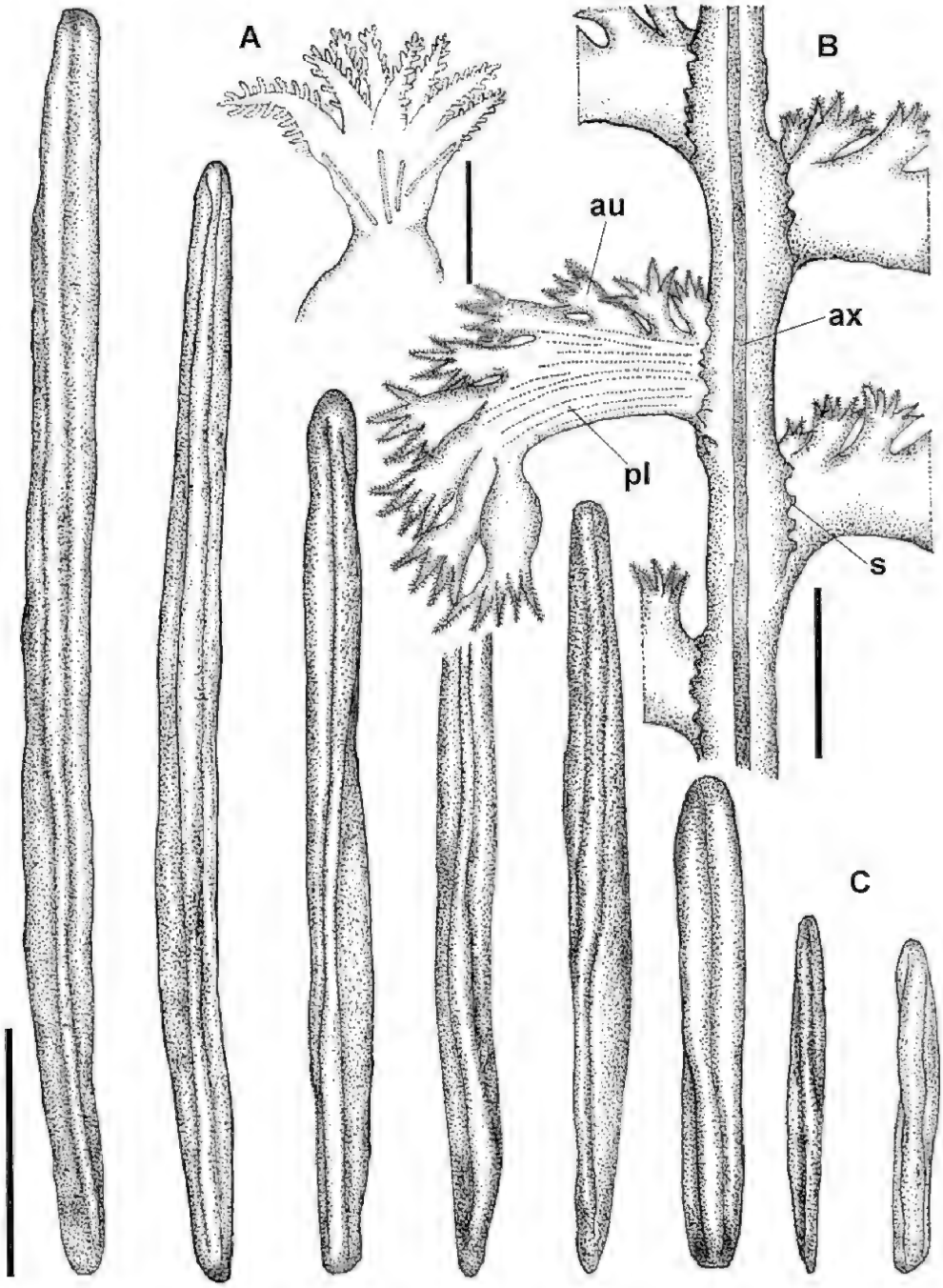

FIGURE 2. *Acanthoptilum longifolium* sp. nov. Polyp leaves and sclerites. A. Individual polyp showing placement of sclerites. B. Portion of rachis showing polyp leaves. C. Polyp leaf sclerites. Abbreviations: au – autozooid; ax – axis; pl - polyp leaf; s – siphonozooid. Scale bars: A = 0.4 mm, B = 2.0 mm, C = 0.1 mm.

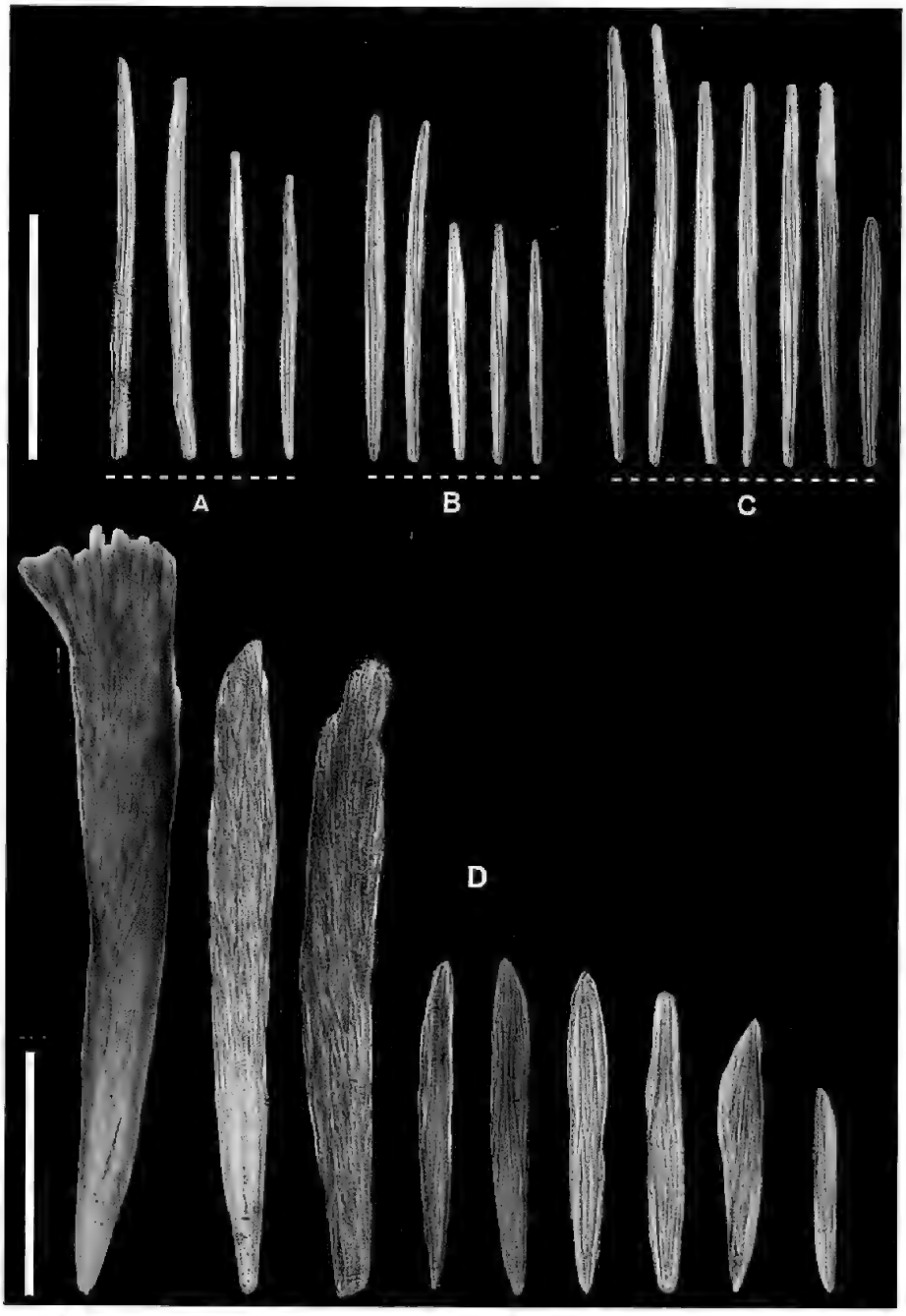

FIGURE 3. Micrographs of sclerites. A-C. *Acanthoptilum longifolium* sp. nov. A. Polyp leaf sclerites. B. Rachis sclerites. C. Peduncle sclerites. D. *Stylatula austropacifica* sp. nov., polyp leaf sclerites. Scale bars = 0.4 mm.

thoptilum album, *A. annulatum*, *A. scalpellifolium*, and *A. gracile*), whereas two are reported from the Gulf of Mexico (*A. agassizii* and *A.pourtalesii*). The new species, *Acanthoptilum longifolium* sp. nov., is known only from New Zealand.

Genus *Stylatula* Verrill, 1864

Stylatula Verrill, 1864:30. Kölliker, 1870: 556. Jungersen, 1904:37. Balss, 1910:42. Kükenthal and Broch, 1911:315. Kükenthal, 1915:67. Bayer, 1961: 307. Williams, 1995:122.

Distribution.— Eastern Pacific Ocean, Atlantic Ocean, New Zealand (Fig. 7).

Stylatula austropacifica sp. nov.

Figures 3D, 4, 5, 7.

Material examined.— Holotype: CAS 173209, Sta. No. NIWA (NZOI) C306, 36°41.00′S 173°58.00′E, 190 m depth, 24 October 1959, one partial colony. Paratype: CAS 173210, Sta. No. NIWA (NZOI) C306, 36°41.00′S 173°58.00′E, 190 m depth, 24 October 1959, one partial colony. Other material: CAS 173211, Sta. No. NIWA (NZOI) B674, 36°40.00′S 173°53.00′E, 196 m depth, 26 October 1962, three partial colonies. CAS 173212, Sta. No. NIWA (NZOI) C306, 36°41.00′S 173°58.00′E, 190 m depth, 24 October 1959, ten partial colonies.

Description of the holotype.— The specimen is comprised of a portion of rachis 120 mm in length, with 37 pairs of polyp leaves. The axis is present throughout the length of the specimen, cylindrical in cross section, ca. 0.8 mm in diameter. Polyp leaves are in pairs, oppositely-arranged, each polyp leaf contains 4–6 autozooids. Tentacles of polyps tightly contracted, wet-preserved polyps tubular/cylindrical, <1.0–1.8 mm long. The polyp leaf fans (basal armatures) are usually composed of 7–8 large sclerites, mostly 1.0–1.3 mm in length. These sclerites are spindles that are not three-flanged, with one end somewhat pointed, whereas the other end is often wider and relatively blunt. The blunt end may be weakly serrated (Figs. 3D, 5B). Longitudinal grooves and ridges are evident on the surface of these sclerites. Four to seven smaller sclerites (0.3–0.5 mm in length) may compose a second fan at the base of the main fan. Polyp leaves are separated by bare areas of rachis, 1.0–1.2 mm in length. Siphonozooids are minute and inconspicuous, longitudinally placed on lateral sides of the rachis below the bases of a particular polyp leaf pair. Retracted polyps light tan in color, rachis white.

Distribution.— West coast of the North Island of New Zealand; 190–196 m in depth (Fig. 7).

Etymology.— The specific epithet is derived from the Latin *australis* (southern) and *pacificus* (Pacific Ocean); in reference to the geographic region of the type locality.

Remarks.— The ten previously described species of *Stylatula* include two from the eastern Pacific, six from the Atlantic (tropical western Atlantic, southwestern Atlantic, Namibia, and Europe), and two species with localities not reported. The new species, *Stylatula austropacifica* sp. nov. is known only from New Zealand.

Stylatula elegans, *S. diadema*, and *S. macphersoni* have numerous (usually more than 8), fine, needle-like sclerites composing the basal armature of a particular polyp leaf. On the other hand, *Stylatula australopacifica* sp,. nov. has a fan-like leaf armature of a few (ca. 7–8) larger, robust, spindle-shaped sclerites, and 4–7 relatively smaller spindles (Figs. 4C–D, 5A–B).

Discussion

The virgulariid genus *Stylatula* was formerly known only from the West Coast of North America, and opposite sides of the Atlantic Ocean, whereas the related genus *Acanthoptilum* was known

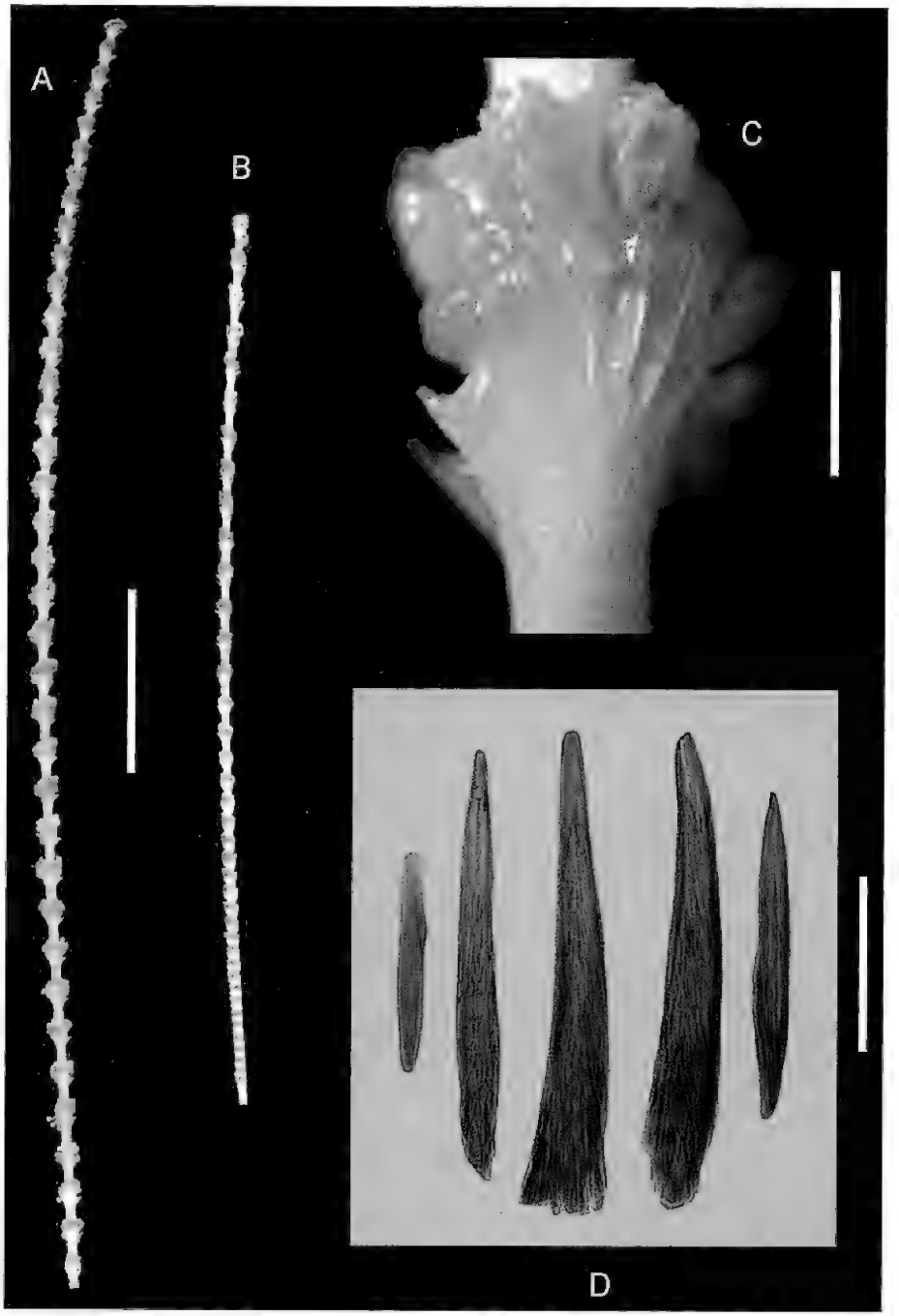

FIGURE 4. *Stylatula austropacifica* sp. nov. A. Holotype, 121 mm long. B. Paratype, 88 mm long; scale bar for A and B = 25 mm. C. A single polyp leaf from the holotype showing subtending fan-like armature; scale bar = 1.0 mm. D. Five scerites from the fan-like armature subtending a polyp leaf of the holotype; scale bar = 0.4 mm.

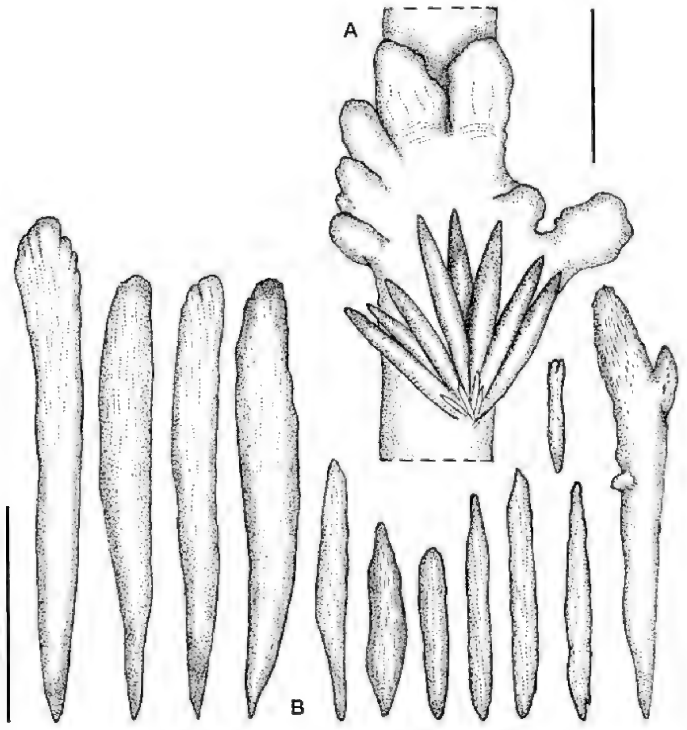

FIGURE 5. *Stylatula austropacifica* sp. nov. A. Portion of rachis showing a single polyp leaf with subtending fan of sclerites; scale bar = 1.0 mm. B. Sclerites from a subtending fan of a polyp leaf; scale bar = 0.5 mm.

only from the west coast of North America and both sides of the Atlantic Ocean. The present paper establishes the presence of these two taxa in the region of New Zealand in the southwestern Pacific Ocean, and provides the descriptions of two new species.

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I express my gratitude to Dennis Gordon, Kareen Schnabel (National Institute of Water and Atmospheric Research – NIWA; formerly known as the New Zealand Oceanographic Institute – NZOI, Wellington), and Steve O'Shea (formerly of NIWA), for their enthusiasm and support, and for making this project possible.

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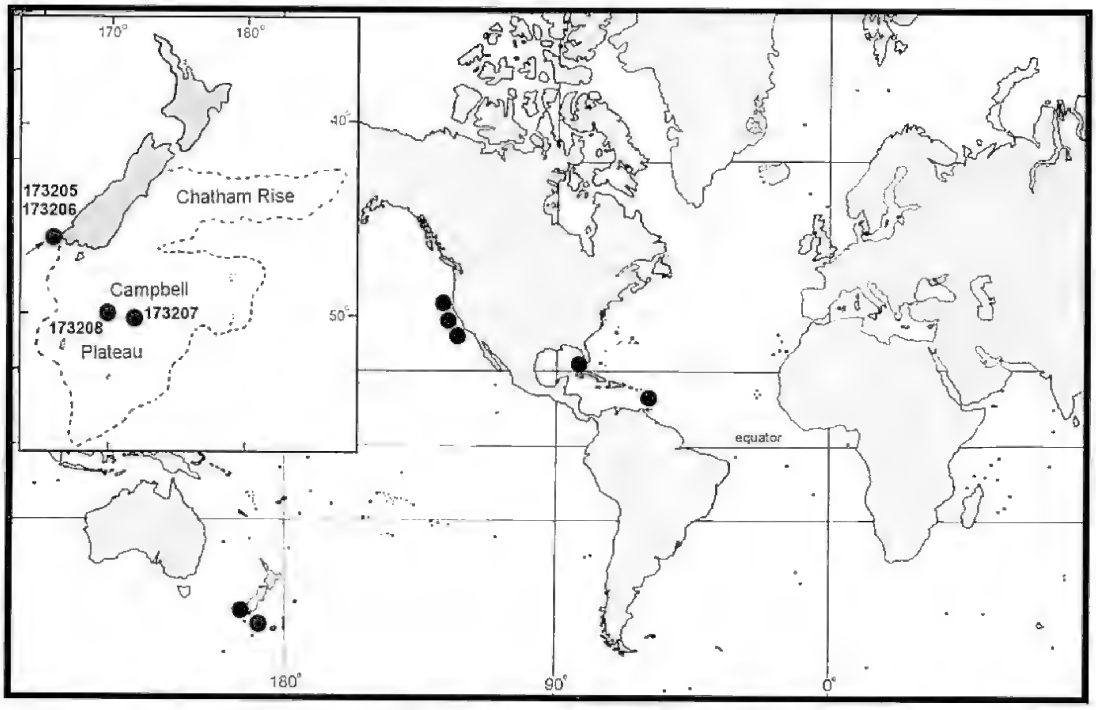

FIGURE 6. World map showing collecting stations (●) for the genus *Acanthoptilum*. Inset: map of New Zealand region showing distribution and type locality (arrow) of *Acanthoptilum longifolium* sp. nov. Six digit numbers refer to CAS catalog numbers.

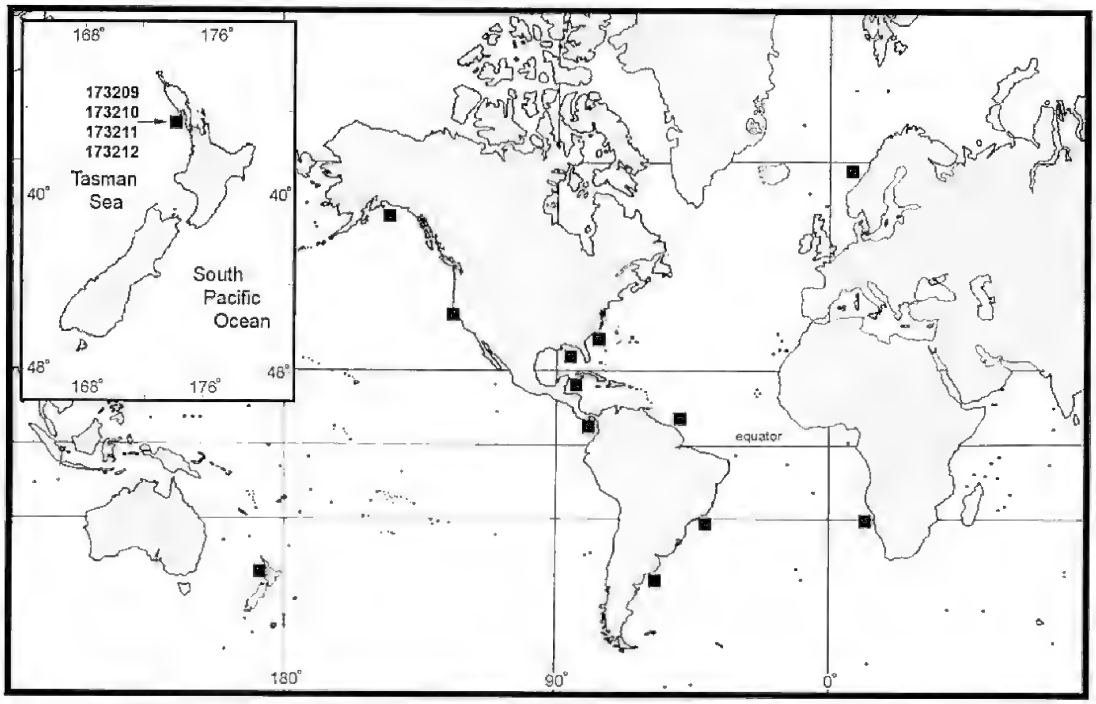

FIGURE 7. World map showing collecting stations (■) for the genus *Stylatula*. Inset: map of New Zealand showing distribution and type locality (arrow) of *Stylatula austropacifica* sp. nov. Six digit numbers refer to CAS catalog numbers.

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New Species of the Spider Genus *Platyoides* from Madagascar (Araneae: Trochanteriidae)

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Two new species of *Platyoides* are described from Madagascar: *P. ravina*, known only from the male, and *P. vao*, known only from the female. The previously unknown male of *Platyoides mailaka* Platnick is newly described and additional records for that species are provided.

In his revision of the trochanteriid genus *Platyoides*, Platnick (1985) described the species *P. mailaka* on the basis of a single female specimen. As a consequence of the ongoing inventory of the Malagasy spider fauna, many additional records of this species have turned up and include many specimens of both sexes. In addition, two other species, here described as *P. ravina* and *P. vao*, are newly discovered.

Materials and Methods

Examination of specimens and drawings was made using a Leica MZ 12.5 Stereo Dissecting Microscope equipped with a camera lucida. Photographs were taken with a Nikon digital camera attached to a Leica MZ16 stereomicroscope and montaged with the Syncroscopy® Auto Montage System. The female epigynum was digested with either KOH under a heat lamp for 3 to 8 hours or a proteinase (trypsin or "ReNu": Enzymatic contact lens cleaner, Bausch & Lomb, Inc.) overnight. For SEM, parts were removed and soaked overnight in 100% EtOH, cleaned with an ultrasonicator, critical point dried with liquid CO_2, sputter coated with AuPd, and scanned with a Hitachi S-520 and Leo 1450VP Scanning Electron Microscope. All available specimens of *Platyoides mailaka*, *P. ravina*, and *P. vao* were measured. All measurements are in mm and were taken using an Olympus SZH10 dissecting microscope. Species distributions were mapped using ArcGIS 9.

Abbreviations used.— AE = anterior eyes, ALE = anterior lateral eyes, ALS = anterior lateral spinnerets, AME = anterior median eyes, AMS = anterior median spinnerets, bc = base of cymbium, c = conductor, CAS = California Academy of Sciences, co = copulatory openings, e = embolus, eb = embolus base, fd = fertilization duct, LE = lateral eyes, ma = median apophysis, MNHN = Museum National d'Histoire Naturelles, MOQ = median ocular quadrangular, MOQAW = median ocular quadrangular anterior width, MOQPW = median ocular quadrangular posterior width, pd = paramedian duct, PLE = posterior lateral eyes, PLS = posterior lateral spinnerets, PME = posterior median eyes, PMS = posterior median spinnerets, rta = retrolateral tibial apophysis, ta = tegular apophysis.

***Platyoides mailaka* Platnick**

Figures 1–5.

Platyoides mailaka Platnick, 1985:15, fig. 47–48. (Female holotype from Antsiranana [= Diégo-Suarez], Madagascar [no date; J. Millot], in MNHN, Paris, not examined).

Material examined.— Madagascar: **Antsiranana Province:** Forêt d'Anabohazo, 120 m, 14°18′32″S, 47°54′52″E, tropical dry forest, beating low vegetation, 11–16 March 2001, B.L. Fisher, C.E. Griswold & al., 1♂, 7 juveniles (CAS), CASENT9007480. Réserve spéciale de l'Ankarana, 80m, 12°54′32″S, 49°6′35″E, tropical dry forest, beating low vegetation, 10–16 February 2001, B.L. Fisher, C.E. Griswold & al., 2 juveniles (CAS), CASENT9006990. **Mahajanga Province:** Parc National d'Ankarafantsika, Forêt d'Ampijoroa, 130 m, 16°19′15″S, 46°48′38″E, 26 March–1 April 2001, tropical dry forest, beating low vegetation, B.L. Fisher, C.E. Griswold & al., 1♀ (CAS), CASENT9007556. Parc National d'Ankarafantsika, Forêt d'Ampijoroa, 130 m, 16°19′15″S, 46°48′38″E, 26 March–1 April 2001, tropical dry forest, general collecting, J.-J. Rafanomezantsoa & al., 1♂ (CAS), CASENTENT9003108. Réserve d'Ankoririka, 210 m, 16°16′2″S, 46°2′55″E, 9–14 April 2001, tropical dry forest, pitfall trap, B.L. Fisher, C.E. Griswold & al, 1♂, 1♀ (CAS), CASENT9007761. Réserve d'Ankoririka, 210 m, 16°16′2″S, 46°2′55″E, 9–14 April 2001, tropical dry forest, sifted litter, B.L. Fisher, C.E. Griswold & al, 2♂, 2♀ (CAS), CASENT9007780.

Diagnosis.— Male most closely resembles that of *Platyoides grandidieri* Simon in having an extremely long retrolateral tibial apophysis (Fig. 1c) but can be distinguished by the form of the embolus, which is thin, straight and with a platelike basal process (curved and without basal process in *grandidieri*); median apophysis long, and stout (short and curved in *grandidieri*); and the presence of a conical sclerotized tegular process (absent in *grandidieri*) (Fig. 1d). Female diagnosed in Platnick, 1985.

Description.— Male (Forêt d'Anabohazo, Antsiranana, Madagascar): Carapace grayish brown, cephalon lighter, black at margins. Chelicerae and pedipalp grayish brown. Legs yellow basally, brownish from patella to tarsi; coxae and trochanters yellowish white. Labium and endites grayish brown, darker basally, slightly lighter apically. Sternum yellow brown, darker near margins. Abdomen yellowish white, dorsum with a U-shaped dark gray median mark, and dark gray marginal bands (Fig. 2a).

Carapace about as long as wide, widest between coxae II and III, narrowed anteriorly, cephalic groove pronounced near eye region, fovea represented by posteriorly pointed thin, deep, and dark triangular depression. Eyes subequal, in two almost straight rows; AE and PLE circular, dark, surrounded by black pigmentation; PME oval, light, not ringed with black; LE on small tubercles; MOQ narrowed in front; clypeus low, about one half diameter of an AME.

Chelicerae laterally divergent, bearing long curved fangs, promargin with one large tooth, retromargin with two dark teeth. Labium slightly longer than wide, narrowed distally, notched basally. Endites obliquely depressed, with long apical scopulae. Sternum flat, scarcely longer than wide, subcircular, truncated at posterior margin, straight along anterior margin, with precoxal sclerites. Abdomen flattened, covered with short setae. Spinnerets small and slightly thinner compared to those of the female, ALS longest, conical, with one large major ampullate gland spigot on the anterior part and four piriforms on the posterior (Fig. 3D); PMS very small with one large minor ampullate spigot on the middle surrounded by three widely separated large aciniforms along the lateral and postero-margin, PLS with one large aciniform spigot; five epiandrous spigots on the epigynal furrow (Fig. 3E); colulus represented by only few setae (Fig. 3F). Legs laterigrade, folded over the body, lacking spines (Fig. 2a–b). Metatarsi and tibiae with single dorsal row of trichobothria; tarsi with two rows of dorsal trichobohria, with two claws, lacking claw tufts, lightly scopulate, with scopulae exending over half length of tibia. Trochanters unnotched, trochanter IV much longer than the others.

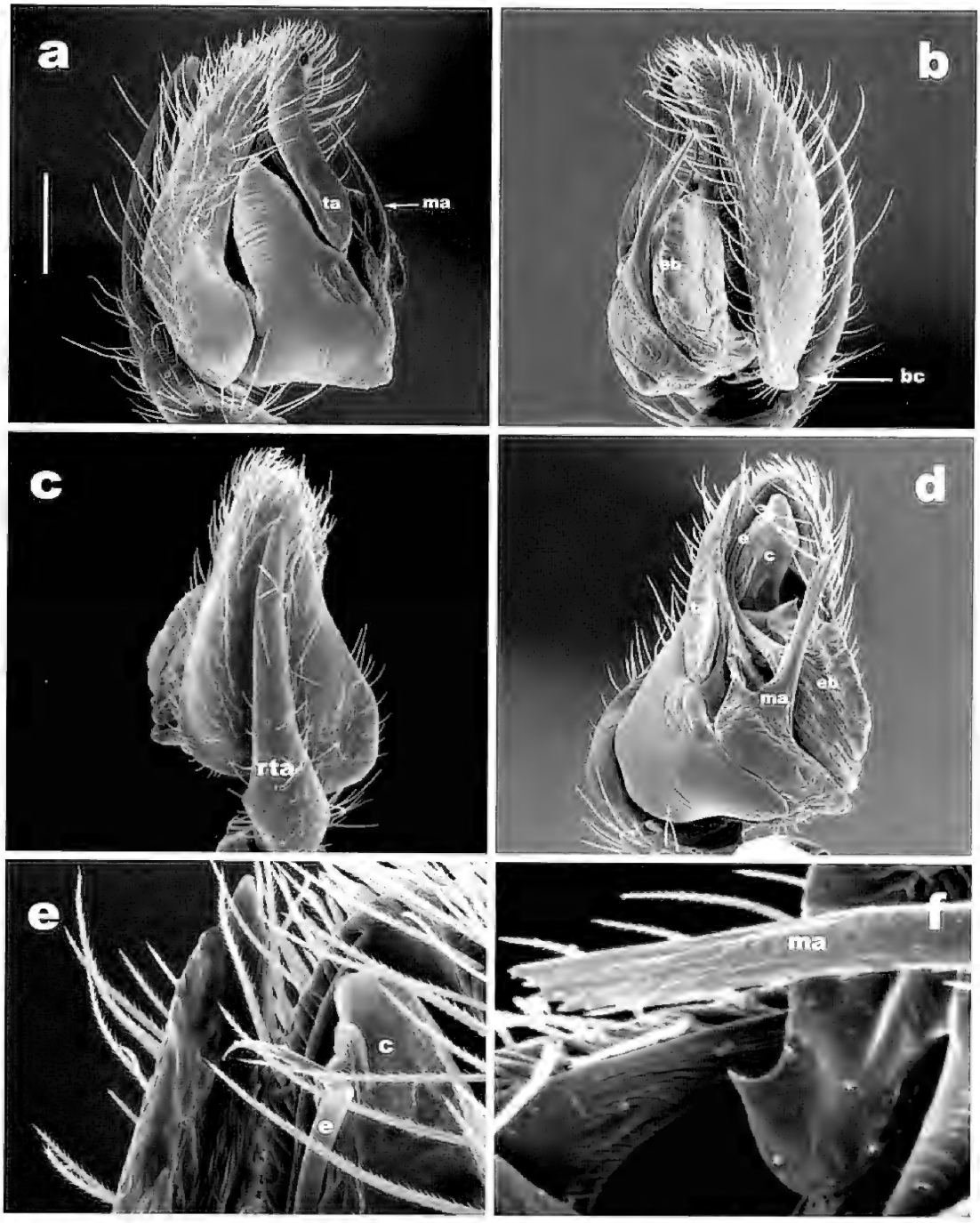


FIGURE 1. *Platyoides mailaka*. Male right palp. a retrolateral. b. prolateral. c. dorsal. d. ventral. E. ventral, close up showing embolus and conductor. f. ventral, close up showing wrinkled tip of median apophysis. Scale bars for a–d = 200µm, e–f = 50µm.

Total length, not including the chelicerae 3.9. Carapace 1.80 long, 1.74 wide. Abdomen 2.10 long, 1.3 wide. Femur II 2.3 long. Eyes sizes and interdistances: AME 0.10, ALE 0.10, PME 0.10; PLE 0.08; AME-AME 0.06, AME-ALE 0.08, PME-PME 0.14, PME-PLE 0.20, ALE-PLE 0.12; MOQ length 0.31, MOQ front width 0.46, MOQ back width 0.59. Palp with long, blunt-tiped retrolateral tibial apophysis, only slightly separated from cymbium (Figs. 1b–c, 4); embolus elongated with semicircular flat disk-shaped base (Figs. 1d, 4); tip of the embolus bent; median apophysis long and thick with wrinkled tip (Fig. 1f); bulb with elongate membraneous conductor and additional conical tegular process (Fig. 1d), base of the cymbium (cb) forming a lobe that is directed outwards (Fig. 1b).

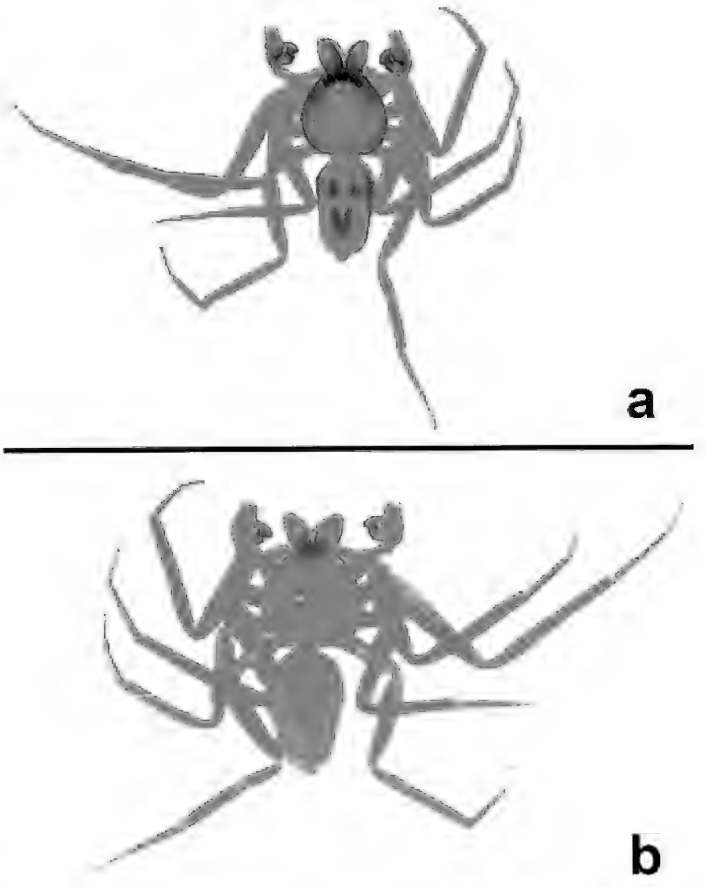


FIGURE 2. *Platyoides mailaka*. Male. a. habitus, dorsal. b. habitus, ventral.

VARIATION.— MALE (n=5): total length 3.8–4.05; carapace length 1.5–1.80; carapace width 1.6–1.75; abdomen length 2.10–2.60; abdomen width 1.10–1.45; ratios of carapace length/width 0.94–1.03; ratios of abdomen length/width 1.51–2.18; ratios of MOQAW/MOQPW 0.77–0.84; ratios of AME/PME 0.83–1.25; ratios of femur II/carapace width 1.25–1.32; ALE 0.08–0.10; PME 0.08–0.12; PLE 0.08–0.10; AME-ALE 0.05–0.08; PME-PME 0.10–0.14; PME-PLE 0.16–0.21; ALE-PLE 0.10–0.12.

FEMALE (described in Platnick 1985). Additional description: (Female from Réserve d'Ankoririrka, Mahajanga, Madagascar): Similar to male, but slightly larger. Color as in male except for one specimen with abdomen completely yellowish white, lacking markings. ALS conical, separated about less than one third of the diameter at base, about two times the length of PLS, with two major ampullate spigots on antero-lateral side and five piriform glands on prolatero-median side (Fig. 3A); PMS very small and hidden by ALS and PLS, bearing 6 cylindrical gland spigots (Fig. 3B); PLS with two large cylindricals on the antero-median side, one giant minor ampullate spigot on the retrolatero-median, surrounded by 12 small aciniform spigots (Fig 3C). Epigynum as shown in Figs. 4.4–4.5. Also described in Platnick (1985).

VARIATION.— FEMALE (n = 4): total length 4.3–4.6; carapace length 1.25–2, width 1.65–1.9; abdomen length 2.05–2.6, width 1.10–1.6. Ratios: femur II/carapace width 0.92–1.33; total length/carapace width 2.38–2.78; MOQAW/MOQPW 0.77–0.82.

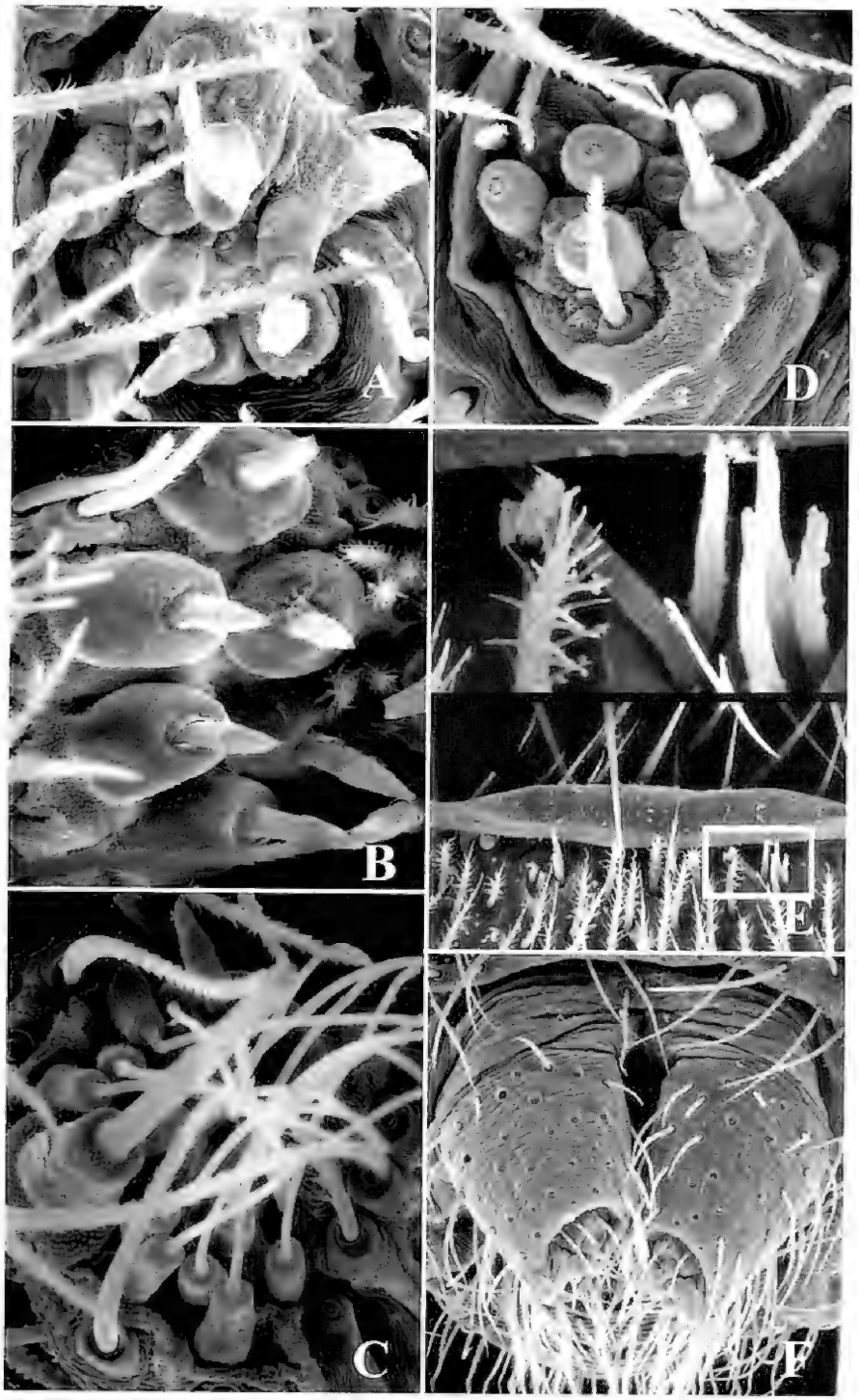


FIGURE 3. *Platyoides mailaka*. Male and female spinning organ. Female. a. right anterior lateral spinneret. b. right posterior median spinneret. c. left posterior lateral spinneret. Male. d. left anterior lateral spinneret. e. epiandrous gland spigots. f. spinnerets, dorsal view. Scale bars for a, d = 20 µm, b, c = 30 µm, e = 43 µm, f = 100 µm.

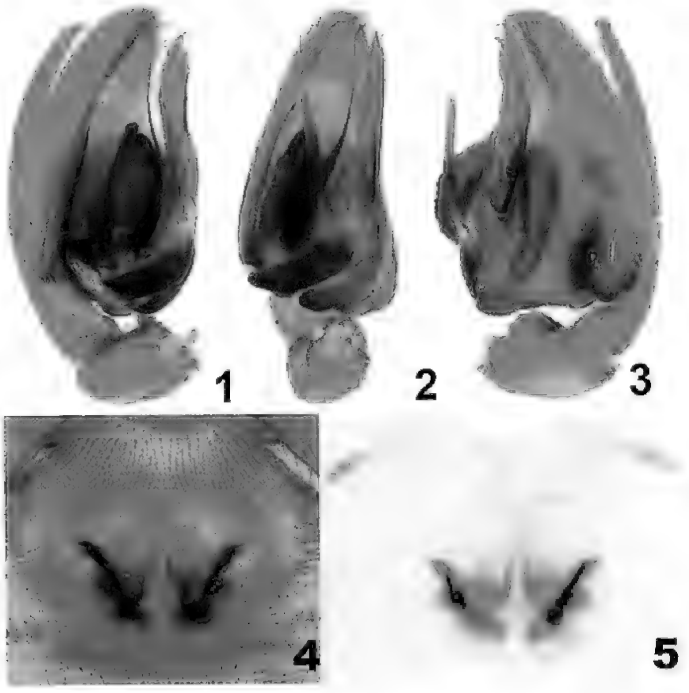


FIGURE 4. *Platyoides mailaka.* Male palp and female epyginum. Male palp. 1. retrolateral. 2. ventral. 3. prolateral. Female epyginum. 4. dorsal. 5. ventral.

FIGURE 5. *Platyoides mailaka, Platyoides ravina, Platyoides vao* distribution in Madagascar.

Note.— The two juveniles from Réserve Speciale de l'Ankarana very closely resemble those of *Platyoides mailaka* in form and color pattern and are tentatively assumed to belong to *mailaka*.

DISTRIBUTION.— Known from northwestern Madagascar (Fig. 5).

Platyoides ravina Andriamalala and Ubick, sp nov.

Figures 6–8.

MATERIAL EXAMINED.— MALES (HOLOTYPE AND PARATYPES). MADAGASCAR: **Tolira Province:** Forêt d'Analavelona, Antanimena, 12.5 km NW Andranoheza, 1500m, 22°40.7′S, 44°11.5′E, transitional mid altitude forest, pitfall traps, 9-15 March 1998, S. Goodman, ♂ holotype and 2 ♂ paratypes (CAS), CASENT 9014022.

ETYMOLOGY.— The species name is from the Malagasy word "Ravina" which means leaf but also refers to a Malagasy pudding "Koba ravina" made with banana fruit, similar to the shape of the embolus in this species.

DIAGNOSIS. — The male can be distinguished from *Platyoides mailaka* Platnick by the short and straight retrolateral tibial apophysis (Figs. 6c, 7.3), the banana shaped embolus (Figs. 6d–e, 7.1–7.2), the median apophysis projecting from a round and flat base (Figs. 6b–f, 7.1–7.3), and palp lacking additional prongs (Fig. 6)

DESCRIPTION. — MALE (Holotype from Forêt d'Analavelona, Antanimena, 12.5 km NW Andranoheza, Toliara, Madagascar): Carapace and chelicerae dark reddish, darkened on margins, pedipalp orange. Legs yellowish orange. Labium and endites orange, slightly lighter apically. Sternum yellowish orange, darker along margins. Abdomen yellowish white, dorsum with a median single longitudinal band, and dark gray on margins (Fig. 8).

Carapace wide (compared to *P. mailaka* male), widest between coxae II and III, narrowed ante-

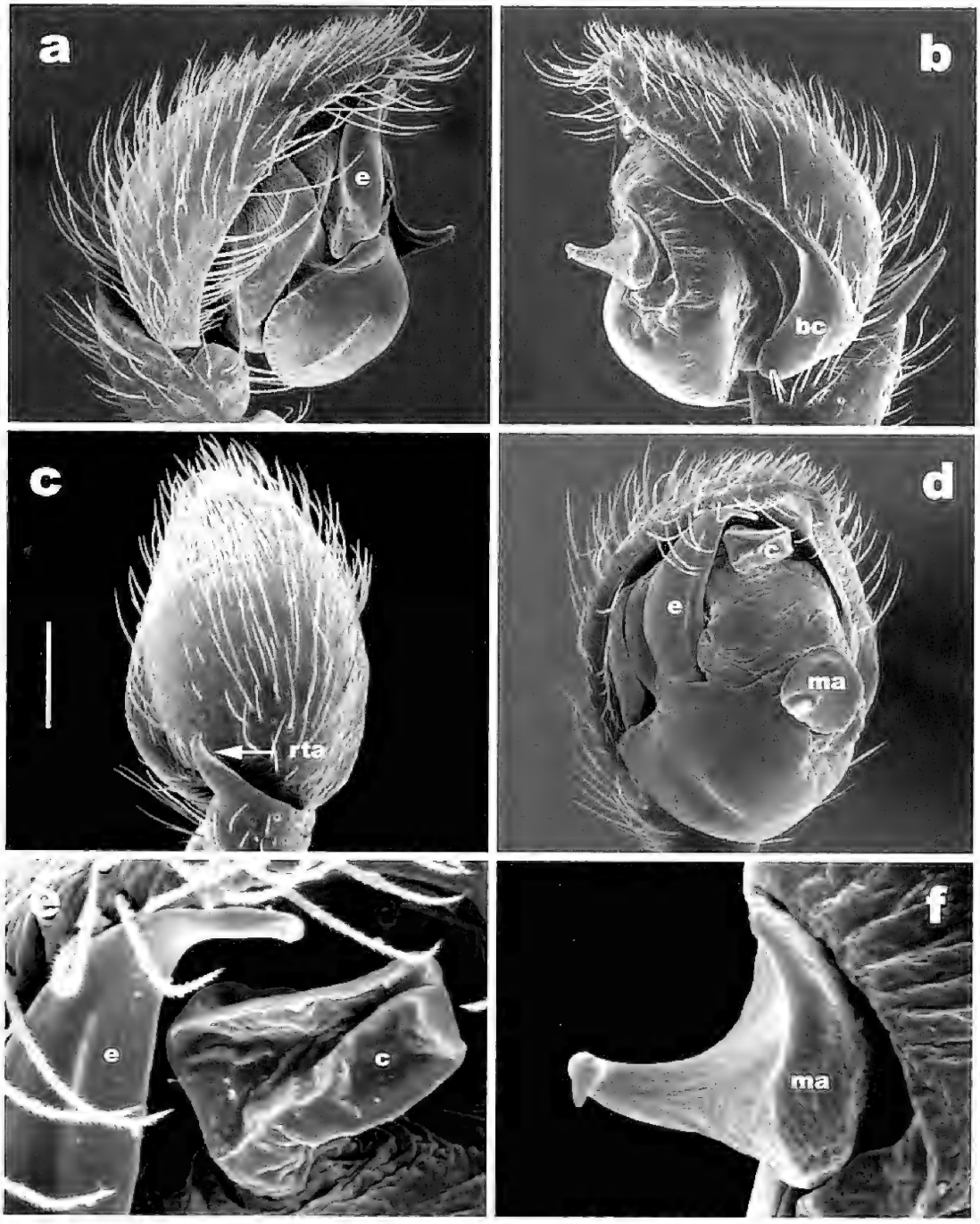


FIGURE 6. *Platyoides ravina*. Male holotype, left palp. a. prolateral. b. retrolateral. c. dorsal. d. ventral. e. ventral, embolus and conductor. f. retrolateral, median apohysis. Scale bars for a–d = 200μm, e = 45 μm, f = 60μm.

riorly, cephalic groove pronounced near eye region, fovea forming posteriorly directed triangular depression. Eyes subequal in size, in two rows, almost straight; AE and PLE circular, dark, and raised on small tubercules; PME oval, light, irregular, and not ringed with black pigmentation; LE

also on small tubercles; MOQ narrowed in front; clypeus low, about one half diameter of an AME. Chelicerae laterally divergent, bearing long curved fangs. Labium longer than wide, not narrowed distally, notched basally. Endites obliquely depressed, with long apical scopulae. Sternum slightly convex, almost circular, with precoxal sclerites. Abdomen flattened, covered with short setae. Colulus represented by only few setae. Legs laterigrade, folded over the body, lacking spines. Metatarsi and tibiae with single dorsal row of trichobothria; tarsi with two rows of dorsal trichobothria, with two claws, lacking claw tufts, lightly scopulate, scopulae exending over half length of tibia. Trochanters unnotched, trochanter IV much longer than the others.

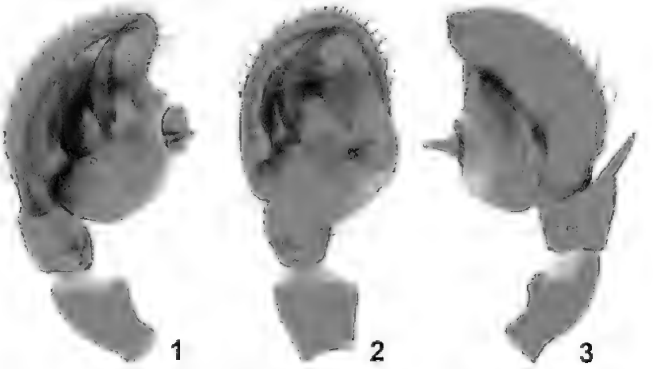


FIGURE 7. *Platyoides ravina*. Male holotype, left palp. 1. prolateral. 2. ventral. 3. retrolateral.

Total length 6 (not including the chelicerae). Carapace 2.6 long, 2.5 wide. Abdomen 3.4 long, 2.1 wide. Femur II 3.3 long. Eyes sizes and interdistances: AME 0.13, ALE 0.12, PME 0.16; PLE 0.14, AME-AME 0.14, AME-ALE 0.14, PME-PME 0.22, PME-PLE 0.28, ALE-PLE 0.12; MOQ length 0.44, MOQ front width 0.44, MOQ back width 0.50. Cheliceral promargin with one large distal tooth, retromargin with two proximal teeth. Palp with a straight, long, blunt-tiped retrolateral tibial apophis, slightly separated from the cymbium; embolus fat and arc like a banana fruit; median apophysis formed by round and flat disque bearing a long projection, which is bent at its apex (Fig. 6f), base of the cymbium forming a large lobe that is oriented toward the tegulum (Fig. 6b).

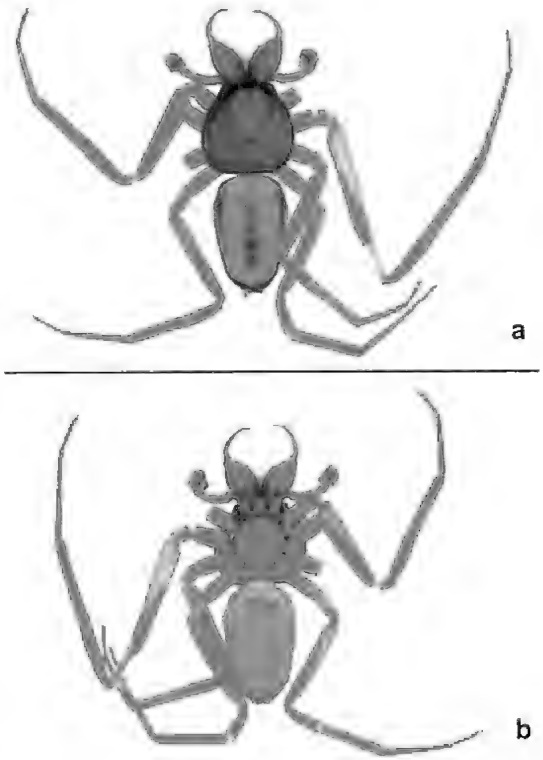


FIGURE 8. *Platyoides ravina*. Male holotype. a. habitus, dorsal. b. habitus, ventral.

VARIATION.— MALE (n = 3): total length 5.3–6; carapace length 2.2–2.7; carapace width 2.2–2.6; abdomen length 3.1–3.5; abdomen width 1.9–2.55; ratios of carapace length/width 1–1.04; ratios of abdomen length/width 1.37–1.63; ratios of MOQAW/MOQPW 0.88–0.9; ratios of AME/PME 0.81–1; ratios of femur II length/carapace width 1.22–1.32; ALE 0.12–0.14; PME 0.14–0.16; PLE 0.12–0.14; AME-ALE 0.09–0.14; PME-PME 0.10–0.14; PME-PLE 0.21–0.24; ALE-PLE 0.12–0.14.

DISTRIBUTION.— Known only from the South of Madagascar (Fig. 5).

***Platyoides vao* Andriamalala and Ubick, sp nov.**
Figures 9–11.

Material examined.— Female (holotype): Madagascar: **Toliara Province**: Réserve Speciale Cap sainte Marie, 12.3 km 262° W of Marovato, 200 m, 25°34′S, 54°11.5′E, spiny forest (thicket), general collecting (ground), 11–15 February 2002, B.L. Fisher et al., 1 ♀ (CAS), CASENT 9012701.

Etymology.— The species name is from the Malagasy word "vao" which means new but also is a common name for a girl.

Diagnosis.— Epigynum distinctive, with one median pair of large globular spermathecae. Posterior ducts widely separated and on lateral sides of spermaphicae. Paramedian ducts anteriorly very long, dilated, curly, and transluscent. Copulatory openings situated posterolaterally (Fig. 9).

Description.— Female (Holotype from Réserve Speciale Cap sainte Marie, 12.3 km 262° W of Marovato, Toliara, Madagascar): Carapace orange brown in the middle and becoming darker to black near margins. Both legs and leg segments are yellowish orange. Labium and endites orange slightly lighter apically. Sternum yellowish orange, slightly convex. Abdomen dark gray, dorsum with multitude of horizontal yellowish stripes and two parallel dark median longitudinal areas. Posterior margins darker (Fig. 10).

Carapace widest between coxa II and III, thoracic groove not well defined, fovea forming a round depression. Eyes in two rows, anterior row slightly recurved, posterior row straight; ALE and PLE circular, dark, surrounded by black pigmentation; PME oval, light, not ringed with black; AME round, slightly darker; LE raised on small tubercles; MOQ narrowed in front; clypeus low, about one half diameter of AME. Chelicerae laterally divergent, bearing long curved fangs promargin with three widely equally spaced medium sized teeth on promargin, and a retromarginal bare (Fig. 11). Labium slightly longer than wide, narrowed distally. Endites obliquely depressed, bearing few hairs at tips. Sternum yellow, slightly darker near margins, slightly convex, scarcely longer than wide, subcircular, truncated at anterior margin, with precoxal sclerites. Abdomen flattened, covered with short setae. Spinnerets small and shorter compared to those *P. mailaka* and *P. ravina*, ALS longest, more or less cylindrical, more closed at their base and then separated at tips. Legs laterigrade, folded over the body, lacking spines and with few setae. Tarsi with a row of dorsal trichobohria, two claws, lightly scopulate, lacking claw tufts. Trochanters unnotched, trochanter IV much longer than the others.

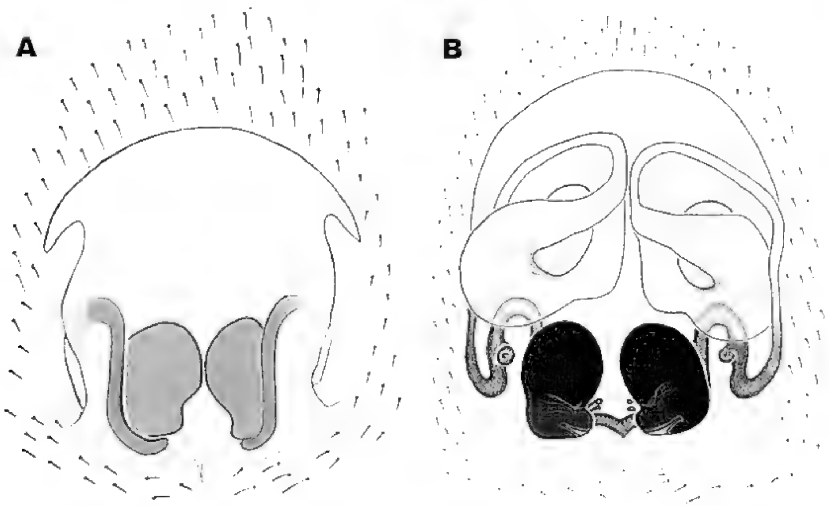
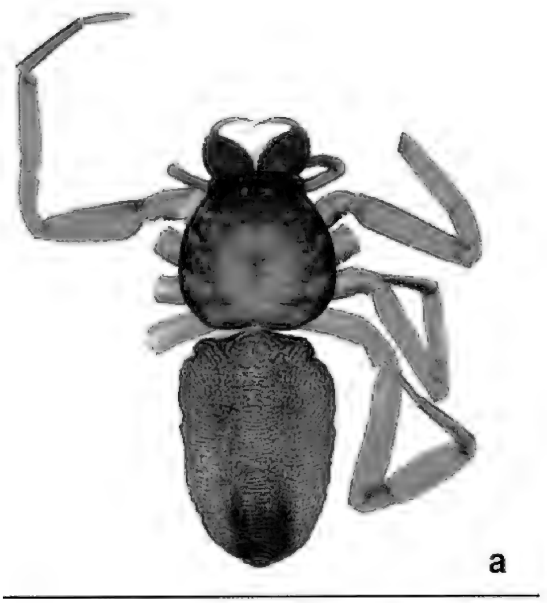


Figure 9. *Platyoides vao*. Female holotype, epyginum. A. dorsal. b. ventral.



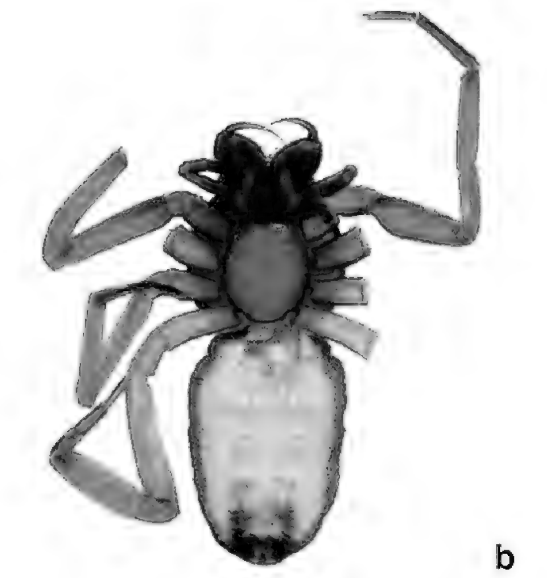


FIGURE 10 (left). *Platyoides vao*. Female holotype. a. habitus, dorsal. b. habitus, ventral.

FIGURE 11 (above). *Platyoides vao*. Chelicerae. Retromargin, showing teeth.

Total length 3.8 (not including the chelicerae). Carapace 1.80 long, 2 wide. Abdomen 3 long, 2 wide. Femur II 1.9 long. Eyes sizes and interdistances: AME 0.10, ALE 0.85, PME 0.80; PLE 0.10; AME-AME 0.06, AME-ALE 0.21, PME-PME 0.21, PME-PLE 0.29, ALE-PLE 0.14; MOQ length 0.27, MOQ front width 0.27, MOQ back width 0.40; ratios of carapace length/width 0.9; ratios of abdomen length/width 1.5; ratios of MOQAW/MOQPW 0.67; ratios of AME/PME 0.12; ratios of femur II length/carapace width 0.95. Chelicerae with three widely equally spaced medium sized teeth on promargin, and a retromarginal bare (Fig. 9).

DISTRIBUTION.— Known only from the South of Madagascar (Fig. 5).

Acknowledgments

Many thanks to the Madagascar Arthropod survey team for their excellent collecting. This research was made possible through the joint collaboration of the California Academy of Sciences, the Botanical and the Zoological park of Tsimbazaza, and the Lakeside Fund for International Students.

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Apogon seminigracaudus, a New Cardinalfish Species Previously Misidentified as *Apogon fuscus* (Teleostei: Apogonidae)

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Apogon seminigracaudus **is a small, red, semitransparent cardinalfish with blackish coloration on the caudal peduncle and lower caudal-fin lobe. This species was first illustrated by Jordan and Seale (1906) and misidentified as *Apogon fuscus* (Quoy and Gaimard). Subsequent workers followed this misidentification, and the species has remained undescribed for over 100 years. *Apogon seminigracaudus* is in the subgenus *Apogon*, and shares a distinctive structure around the anterior nostril with *A. dorysa*, *A. lativittatus*, and *A. semiornatus*. It has 13 pectoral-fin rays, usually 4 + 14 gill rakers, and one and a half scales between the lateral line and center of the first dorsal fin. It is known from Japan, Ryukyu Islands, Ogasawara Islands, Fiji, Tonga, and Samoa.**

In 1906, Jordan and Seale, in their *Fishes of Samoa*, illustrated a cardinalfish they identified as *Amia fusca* (Quoy and Gaimard) (Jordan and Seale 1906:244, fig. 38) (Fig. 1). They had a single specimen from Apia. This illustration shows a fish with black markings on the caudal peduncle and lower half of the caudal fin, and they commented on its distinct coloration. Subsequent to their identification of their specimen as *Amia fusca*, later workers followed suit and used the name *Apogon fuscus* for this species (Kuiter and Kozawa 1999; Hayashi 2002).

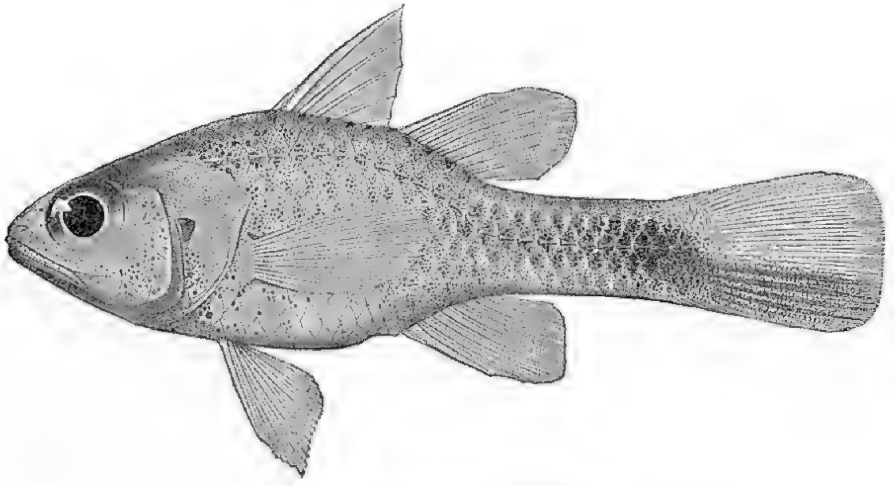

FIG. 38.—*Amia fusca* (Quoy & Gaimard).

FIGURE 1. Figure 38 of *Amia fusca* (Quoy and Gaimard) from Jordan and Seale (1906).

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While conducting a survey of the marine fishes of Fiji, I collected over twenty lots of this small, red cardinalfish with a blackish caudal peduncle and black pigment on the lower half of the caudal fin. In attempting to identify these specimens, I investigated the name *A. fuscus* that had previously been applied to this species. Because the name *fuscus* has also been associated with the *Apogon bandanensis* group (Myers 1989), I contacted T.H. Fraser who is revising that group, and he informed me (pers. commun., 31 Jan. 2007) that in a future publication he will be treating *A. fuscus* as a valid species within the *bandanensis* group. Earlier, I had concluded that the use of *A. fusca* by Jordan and Seale (1906) was a misidentification (Greenfield 2001).

In a revision of the *Apogon erythrinus* complex (Greenfield 2001), I discussed all of the semitransparent red cardinalfish species that have been described. The only name that is not accounted for is *Apogon arenatus* Bleeker (1859–60). Bleeker based his description on a drawing by Castelnau (location unknown), and there is no holotype. The color description Bleeker gives does not match that of the species in question, which was first illustrated by Jordan and Seale (1906). Three additional recently described species, *Apogon lativittatus* (Randall, 2001) and *Apogon kauteame* and *Apogon rubrifuscus* (Greenfield and Randall, 2004), also are not this species. Thus, although this species has been illustrated several times, it remained undescribed for over 100 years. The purpose of this paper is to describe the species as *Apogon seminigracaudus*.

Materials and Methods

All counts and measurements follow Hubbs and Lagler (1964) except that the last two fin rays of the dorsal and anal fins are not counted as one unless it is clear that they are joined at the base. Also, caudal-peduncle length is measured horizontally not obliquely. Measurements were made to the nearest 0.1 mm using dial calipers and are expressed as percentage of standard length (SL). Length of dorsal-fin spines was measured by placing one end of the caliper tip at the base of the spine pushed against the posterior base of the spine anterior to it and the other caliper tip at the spine tip. Gill-raker counts include rudiments. Data for the holotype are presented first, followed by values for all specimens in parentheses if different. Institutional abbreviations are as listed in Leviton et al. (1985).

Species Description

***Apogon seminigracaudus* Greenfield, sp. nov.**
Figures 1–4.

Material Examined.— Holotype: CAS 224639 (Fig. 2), 29.7 mm SL. Fiji, N. shore of Vanua Levu, reef N.E. of Yaqaga Id. and N.W. of Ovatoa Reef, 16°30.717′S, 178°38.730′E, 14 m, isolated patch reef on sand flat, 25 March 2002, field number G02-105, rotenone, collected by D.W. Greenfield, R.C. Langston, K.R. Longenecker. Paratypes: CAS 224640, 32.6 mm, Fiji, Viti Levu, Nasava Bay, 17°29.442′S,178°21.171′E, 5.6–8.0 m, fringing reef, 4 November 2002, field number G02-143, rotenone, D.W. Greenfield, K.S. Cole, R.C. Langston, K.R. Longenecker; CAS 224641, 30.3 mm. Fiji, N. shore of Viti Levu, Nananu-i-Ra, 17°16.704′S, 178°12.932′E, 3.1–5.8 m, fringing reef, 15 November 2002, field number G02-186, rotenone, D.W. Greenfield, K.S. Cole, R.C. Langston, K.R. Longenecker; AMS I.44090-001, 27.7 mm, taken with CAS 224641; BM(NH) 2007.4.4.1, 29.9 mm, taken with CAS 224641; BPBM 40508, 32.6 mm, Fiji, E. coast of Vanua Levu, Nasau Bay, 16°43.650′S,179°53.970′E, 0.31–3.1 m, patch reef, 25 May 2003, field number G03-61, rotenone, D.W. Greenfield, T.A. Greenfield; FMNH 117287, 31.9 mm. Same location as holotype, 25 March 2002, field number G02-104, rotenone, D.W. Greenfield, R.C. Langston, K.R. Longenecker, B.K. Mataitini; NSMT-P 76275, 30.3 mm, taken with FMNH 117287; SAIAB (RUSI) 79500, 30.4 mm, taken with CAS 224641; USNM 389555, 31.4 mm, taken with BPBM 40508.

Apogon seminigracaudus (non-type material): Fiji: CAS 224642(1), CAS 224643(2), CAS 224644(1),

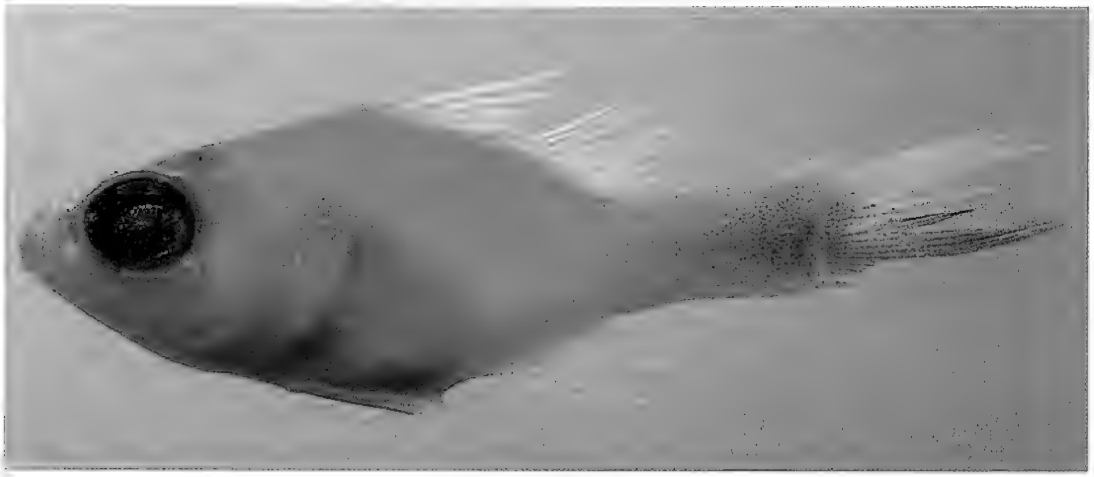

FIGURE 2. Holotype of *Apogon seminigracaudus* Greenfield, CAS 224639, 29.7 mm SL.

CAS 224645(1), CAS 224646(2), CAS 224647(1), CAS 224648(5), CAS 224649(5), CAS 224650(1), CAS 224651(1), CAS 224652(3), CAS 224653(2), CAS 224654(2), CAS 224655(3), CAS 224657(2), CAS224658(1), USNM 245650(1). Tonga: USNM 341780(2), USNM 341781(3).

Apogon lativittatus (PARATYPES): BPBM 11032 (5), Marquesas Islands.

Apogon semiornatus: BPBM 23453(2), Philippine Islands; BPBM 32375(2), Indonesia.

Apogon doryssa: CAS 224659(3), Fiji.

DIAGNOSIS.— A small, usually less than 33 mm SL, semitransparent, red species with a blackish stripe on the center of the caudal peduncle, extending posteriorly onto the lower half of the caudal fin; with six spines in the first and one spine and nine rays in the second dorsal fin; two spines and eight rays in the anal fin; 13 pectoral-fin rays; 4–5 + 13–15 (usually 4 + 14) gill rakers (rudiments included) on the first gill arch; one scale (plus ½ sometimes) between the lateral line and the base of the third spine of the first dorsal fin; anterior nasal opening lacking a posterior flap and with an indentation in the skin below it (Fig. 3); two predorsal (supraneural) bones.

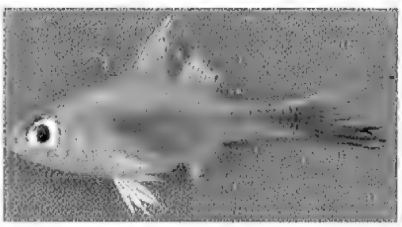

FIGURE 3. Fresh color of *Apogon seminigracaudus* Greenfield, CAS 224642, 35.0 mm SL.

DESCRIPTION.— Dorsal-fin elements VI-I,9; anal-fin elements II,8; all dorsal and anal soft rays branched, the last to base; pectoral-fin rays 13, upper two and lower one unbranched; pelvic rays I,5; lateral line complete, the pored scales 24; predorsal scales 6; scales above lateral line to center of first dorsal fin one (plus ½ sometimes); transverse scales 10; circumpeduncular scales 12; gill rakers 4+14 [4+13(5), 4+14(11), 5+14(2), 5+15(2)], in the holotype two developed and two rudimentary on the upper arch and four rudimentary and 10 developed on the lower arch. Gill raker counts based on 10 types plus 10 nontype specimens.

MEASUREMENTS (based on holotype and nine paratypes): Measurement for holotype presented first, followed by range for all types and the mean in parentheses, all in percentage of SL. Standard length 27.7–32.7 mm. Greatest body depth 35.5 (32.0–35.5, 33.8). Body width 16.8 (15.6–18.1, 17.0). Head length 38.9 (38.0–40.8, 39.2). Snout length 7.4 (5.8–7.8, 6.9). Orbit diameter 14.8 (12.1–15.1, 13.9). Bony interorbital width 7.1 (7.1–10.0, 8.1). Upper-jaw length 20.9 (18.3–24.4, 21.1). Caudal-peduncle depth 12.6 (10.8–12.6, 11.8). Caudal-peduncle length 30.6 (26.4–30.6,

28.8). Predorsal length 40.7 (40.3–44.9, 42.1). Preanal length 58.2 (55.1–60.9, 58.7). Prepelvic length 35.0 (31.4–39.0, 34.3). First dorsal-fin spine length 5.2 (5.2–7.7, 6.6). Second dorsal-fin spine length 27.9 (25.4–27.9, 26.5). Third dorsal-fin spine length 24.6 (17.8–24.6, 21.2). Length of spine of second dorsal fin 16.2 (13.8–16.2, 15.1). Longest dorsal ray 25.9 (1st) (22.3–28.3, 24.6 (1st or 2nd). First anal-fin spine 5.7 (4.3–5.9, 5.0). Second anal-fin spine 15.8 (14.1–18.5, 15.8). Longest anal ray 23.6 (1st) (20.7–25.0, 22.6 [1st or 2nd]). Last anal ray 12.1 (9.9–14.5, 11.5). Caudal-fin length 35.2 (29.4–35.2, 32.2). Caudal-fin concavity 14.0 (10.3–14.1, 12.1). Pectoral-fin length 30.3 (24.0–30.3, 27.2). Pelvic-spine length 22.0 (18.4–22.0, 20.2). Pelvic-fin length 29.3 (24.8–29.3, 26.3). Caudal fin is forked; the illustration in Jordan and Seale (1906) is in error showing a rounded caudal fin.

Color (of fresh specimen; from 35mm transparency of CAS 224649): Head and body semitransparent, overlaid with a wash of pink anteriorly and red posteriorly. Abdomen silvery in sharp contrast to the rest of the body. Red color of gill filaments showing through opercular area. Scales along back and sides with dark pigment in the central portion, resulting in a pattern of crescents. Blackish pigment increasing posteriorly along the caudal peduncle becoming black at caudal-fin base and onto the lower caudal-fin lobe. The upper caudal-fin lobe and all other fins red. Outer rim of orbit with a dark edge, pupil black and iris bright silver. Kuiter and Kozawa (1999) have an underwater photograph of this species from Kerma, Japan, on page 80 of their CD. Their photograph shows a bluish tinge to the dark scales on the nape and also on the iris of the eye.

Color (in alcohol): Head and body straw colored. Area over brain brown. Predorsal scales and scales along base of first two spines of first dorsal fin with heavier brown pigment. Sides of the head and body above level of pectoral fin with a lighter peppering of brown pigment. Caudal peduncle with heavier brown pigment, intensifying towards caudal-fin base, and extending onto lower lobe of caudal fin. Upper caudal-fin lobe and all other fins clear. Iris of eye black, pupil dark straw.

Etymology.— The specific epithet is a compound adjective from the Latin, *semis* (half), *niger* (black), and *cauda* (tail) in reference to the black pigment on the lower half of the caudal fin.

Habitat.— *Apogon seminigracaudus* was collected in Fiji between 0.3 and 15 meters. A single specimen was collected at 30.1 m in Fiji by V.G. Springer. In examining field data for 20 different collections, all were either from patch reefs on sand or at fringing reefs close to shore. Almost all stations had comments about one or more of the following conditions: silty or fine sand, heavy silt, heavy algae, dead coral, and bleaching. It thus appears that this species does not usually occur in more pristine coral-reef habitats.

Range.— Hayashi (2002) reports this species from Japan, Ryukyu Islands, and the Ogasawara Islands. It is recorded from Fiji in this paper, and specimens from the Tonga Islands (USNM 341780 and 341781 misidentified as *A. semiornatus*) have been examined. Jordan and Seale (1906) illustrated this species from Samoa.

Comparisons.— *Apogon seminigracaudus* belongs to a group of small, red, semitransparent species in the subgenus *Apogon*. Greenfield (2001) recognized two phenetic groups among these fishes, both defined by the structure of the snout around the anterior nostril and the number of scales between the lateral line and the first dorsal fin. In the *erythrinus* complex, containing *A. erythrinus*, *A. indicus*, *A. marquesensis*, and *A. susanae*, the skin at the end of the snout covers the nasal bones and extends over the ascending process of the premaxilla smoothly with no free edge near the anterior nasal opening, and two large, full, scales between the lateral line and first dorsal fin (Greenfield 2001: Figs. 1A, C, G). In the *coccineus* complex, containing *A. crassiceps* and *A. campbelli*, there is a free edge of skin near the anterior nasal opening (a flap), and only a single large, full scale between the lateral line and the first dorsal fin (Greenfield 2001: Figs. 1B, D, F). A smaller half scale may be present in addition to the full scales in both complexes. Greenfield and Randall (2004)

described another species from Easter Island, *A. kauteamea*, that has the nasal flap of the *coccineus* complex, but has two scales between the lateral line and the first dorsal fin. They then redefined the two complexes only on the basis of nasal structure.

Apogon seminigracaudus has a nasal structure that differs from both the *erythrinus* and *coccineus* complexes (Fig. 4), and shares this pattern with *A. lativittatus*, *A. semiornatus*, and *A. doryssa*. The ventral edge of the preorbital that overlaps the premaxilla extends anteriorly to under the anterior nostril where there is an indentation. There is no flap posterior to the nostril as in the *coccineus* complex, nor is the lower edge smooth and continuous as in the *erythrinus* complex. Just anterior to the nostril is a free flap that extends ventrally with an opening in it where a probe may be inserted. Again, this is only a phenetic grouping and there is no evidence that this is a shared derived character.

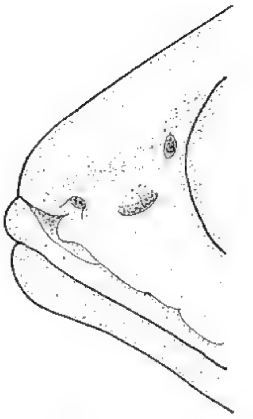

FIGURE 4. Snout morphology of Apogon seminigracaudus, CAS 22460, paratype, 32.6 mm SL.

In terms of coloration, only *A. doryssa* lacks some blackish pigmentation on the body. The other three species have different patterns of blackish areas on the body. *Apogon lativittatus* has a blackish area along the lateral line on the caudal peduncle that runs onto the center of the caudal fin. *Apogon semiornatus* also has blackish pigmentation along the lateral line of the caudal peduncle extending onto the center of the caudal fin, but also has a blackish band extending from the eye posteriorly onto the opercle, and another band from the pectoral-fin base to the anal fin. *Apogon seminigracaudus* has blackish pigmentation on the caudal peduncle running along the lateral line, but it extends posteriorly only onto the lower half of the caudal fin.

Apogon seminigracaudus further differs from *A. doryssa* by having 13 pectoral-fin rays instead of 11–12. It differs from *A. semiornatus* by having 13 pectoral-fin rays (all 20 specimens), whereas Randall (2001) states that of 21 specimens of *A. semiornatus*, 19 had 12 rays and only two had 13. *Apogon semiornatus* also has 12–13 gill rakers on the lower arch, whereas *A. seminigracaudus* usually has 14. *Apogon lativittatus* differs from *A. seminigracaudus* by being a larger species (to 58.4 versus 32.6mm SL for the largest *A. seminigracaudua*) and by having two and a half scales between the lateral line and the center of the first dorsal fin versus one and a half. It also has 12–13 gill rakers on the lower arch rather than 14, and has a deeper body (33.0–38.8, mean = 35.7% SL versus 32.0–35.5, mean = 33.8% SL). Most obviously it differs from all apogonid species by its distinctive coloration.

Randall (2005) reported that *Apogon semiornatus* occurs in the Indian Ocean and southern Japan to the Great Barrier Reef and New Caledonia, and no other localities in Oceania, and *A. lativittatus* is known only from the Marquesas Islands. *Apogon doryssa* is more widespread, ranging from the Indian Ocean across to the Tuamotu Archipelago. It is likely that specimens from Oceania identified as *A. semiornatus*, like those from Tonga at the USNM (Randall et al. 2003), might in fact be *A. seminigracaudus*.

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The California Academy of Sciences Gulf of Guinea Expeditions (2001, 2006) VI. A New Species of *Phrynobatrachus* from the Gulf of Guinea Islands and a Reanalysis of *Phrynobatrachus dispar* and *P. feae* (Anura: Phrynobatrachidae)

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The oceanic islands of São Tomé and Príncipe in the Gulf of Guinea of Africa harbor a surprising number of endemic amphibians. Two species of puddle frogs (*Phrynobatrachus*) have been described from these islands: *Phrynobatrachus dispar* (Peters, 1870) and *P. feae* (Boulenger, 1906). The validity of *P. feae* as a taxon distinct from *P. dispar* has been in doubt and in recent works the two have been considered synonymous. However, a detailed analysis has never been performed. We examined 175 specimens of *Phrynobatrachus* collected from the two islands during the 2001 and 2006 CAS Gulf of Guinea expeditions as well as two syntypes of *P. feae*. Consistent external morphological and osteological differences were found between specimens from different islands. Furthermore, maximum likelihood analysis of cytochrome b sequences revealed a high mean inter-island sequence divergence of 21%, whereas intra-island distances were only around 1%. This level of divergence indicates an ancient split, possibly predating the formation of São Tomé. Mitochondrial DNA sequences from 12S rRNA, valine-tRNA, and 16S rRNA genes support this divergence and indicate that the *P. dispar* clade is sister to an East African clade of *Phrynobatrachus*, and not West African species, a recurrent theme with this insular amphibian fauna. Because the type localities of both currently available names are on Príncipe Island, the species endemic to São Tomé is undescribed. We thus describe a new species of *Phrynobatrachus*, raising the current total of endemic amphibian species in the Gulf of Guinea Islands from six to seven.

As ilhas oceânicas de São Tomé e Príncipe no Golfo de Guiné da Africa, abrigam um número significativo de anfíbios endêmicos. Duas espécies de rãs que vivem em poças d'água (*Phrynobatrachus*) foram descritas nestas ilhas: *Phrynobatrachus dispar* (Peters, 1870) e *P. feae* (Boulenger, 1906). A validade de que *P. feae* é um taxon distinto de *P. dispar* esteve em dúvida e, em um trabalho recente, as duas espécies foram consideradas a mesma. No entanto, um detalhe na análise nunca foi executado. Nós examinamos 175 espécimes de *Phrynobatrachus* coletados nas duas ilhas, incluindo os dois syntypes de *P. feae*, durante as expedições da California Academy of Sciences no Golfo da Guiné, em 2001 e 2006. Diferenças morfológicas externas e osteológicas

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foram observadas entre os espécimes de ilhas diferentes. Além disso, a análise da probabilidade máxima das seqüências do citocromo b revelaram uma média alta de divergência inter-ilha de 21%, enquanto as distâncias intra-ilha foi ao redor de 1%. Tal nível de divergência indica uma separação muito antiga, possivelmente pré-datando a formação de São Tomé. As seqüências de ADN mitocondrial do rRNA 12S, tRNA-valina, e genes rRNA 16S confirmam esta divergência e indica que o clade *P. dispar* é proveniente do clade africano do leste de *Phrynobatrachus*, e não da espécie Africana do oeste. Considerando que as duas espécies já nomeadas estão localizadas na Ilha de Príncipe, as espécies endêmicas a São Tomé não estão devidamente representadas. Sendo assim, nós descrevemos uma espécie nova de *Phrynobatrachus*, aumentando o número total de espécies endêmicas de anfíbios no Golfo das Ilhas de Guiné de seis para sete.

The oceanic islands in Gulf of Guinea archipelago contain some of the highest levels of endemicity in the world, including six currently recognized endemic amphibian species. São Tomé and Príncipe lie 280 km and 220 km off the coast of mainland Africa respectively, with ocean depths between the continent and the islands reaching 4000 m. Geologic evidence indicates these two islands and out-lying Annobon have never been connected to the mainland, which suggests dispersal as the most likely mechanism for colonization (Measey et al. 2007). Traditionally, transoceanic dispersal by amphibians is thought to be highly unlikely because of low physiological tolerances for salinity, and the presence of endemic amphibians of the Gulf of Guinea islands, including the fossorial caecilian *Schistometopum thomense*, has been among the most remarkable and perplexing biogeographic mysteries. Nevertheless, several recent studies suggest that transoceanic dispersal of amphibian species must have occurred (Fahr 1993; Vences et al. 2003; Vences et al. 2004; Measey et al. 2007).

The diminutive anurans of the genus *Phrynobatrachus* (Günther 1862) are notoriously difficult to distinguish morphologically. These species are generally highly polymorphic, quite small in size, cryptically colored, and often have limited descriptions in the literature (Stewart 1974; Drewes and Perret 2000; Hoffman and Blouin 2000; Crutsinger et al. 2004). Consequently, we understand little about this widespread genus, which is among the most speciose of African anurans.

Two species of *Phrynobatrachus* have been described (as *Arthroleptis* Smith) from the Gulf of Guinea islands of São Tomé and Príncipe: *P. dispar* (Peters 1870) and *P. feae* (Boulenger 1906). Type localities for both species are given as the island of Príncipe, although the range of *P. dispar* was later expanded to include São Tomé (Loumont 1992). Boulenger gave very few characters to define *P. feae* as a species distinct from *P. dispar.* Peters described *P. dispar* as being 20 mm snout-vent length (SVL) whereas Boulenger indicated the maximum length for 25 specimens of *P. feae* as 12 mm and 15 mm SVL for males and females respectively. Furthermore, only one character is provided in Boulenger's dichotomous key to distinguish the two species:

> ...inner metatarsal tubercle considerably nearer to the outer than to the tarsal tubercle . . . . . *A. dispar*
> ...inner metatarsal tubercle tubercle equally distant from the outer and from the tarsal tubercle . . . . . *A. feae*

Since then, only limited attention has been given to the Gulf of Guinea *Phrynobatrachus.* Loumont (1992) found that the spacing between tubercles was unreliable and seemed to vary with ontogeny, and that it was unlikely that two species could occupy the same niche on the small island of Príncipe. *Phrynobatrachus feae* has been treated as a junior synonym of *P. dispar* by subsequent

authors (Loumont 1992; Schätti and Loumont 1992; Drewes and Stoelting 2004; Frost 2004).

Jonathan Baillie (1999) observed *Phrynobatrachus* at all elevations on Príncipe and noticed that there seemed to be two distinct size classes: a small size class congregating by the rivers at night and a larger size class seen inhabiting the forest. He also suggested that there might be more polymorphism among Príncipe populations than in populations from São Tomé, suggesting the possible existence of two species on Príncipe. Baillie also speculated that *P. feae* may simply be juvenile *P. dispar* or, if a distinct species, that the former might be a dwarfed form of *P. dispar*.

Loumont (1992) stated that amphibians occur in two ecological zones on the islands, a low elevation zone from 0–500 m where *Phrynobatrachus was* found, and a middle montane zone from 500–1000 m. However, both Baillie (1999) and Drewes and Stoelting (2004) observed *Phrynobatrachus* at considerably higher elevations than previously reported on both São Tomé and Príncipe, including on the summit of Pico de Príncipe at 948 m and at an elevation of 1412 m on São Tomé; therefore, the possibility exists that two species of *Phrynobatrachus* might inhabit the same island by occupying different elevational zones.

For this study, we examined the largest collection of Gulf of Guinea *Phrynobatrachus* in existence. Specimens were taken at multiple elevations on both islands and analyzed using a combined dataset of morphological, osteological and molecular characters. The datasets provide compelling evidence for the recognition of two distinct species of *Phrynobatrachus*, each endemic to a single island. Because the type locality of both *P. dispar* and *P. feae* is Príncipe Island, we herein describe a new species endemic to the island of São Tomé and raise the number of recognized amphibian species from the oceanic islands in the Gulf of Guinea islands to seven.

Materials and Methods

Collection of specimens.— One hundred and fourteen individuals were collected during the California Academy of Sciences' (CAS) first Gulf of Guinea Expedition (March–June, 2001) and an additional 61 frogs were collected during the second expedition, March–June 2006. Specimens were hand collected, euthanized and preserved in 10% formalin (Drewes and Stoelting 2004). Sixty-four individuals from 10 localities were collected from São Tomé and a total of 112 individuals from 10 localities were collected from Príncipe (Fig. 1; Appendix Table 1). The sample is heavily biased toward calling males because these are easier to locate in the field. Tissue samples, taken from 25 individuals from seven localities on São Tomé and 19 individuals from four localities on Príncipe, were placed in 95% ethanol. Institutional abbreviations follow Leviton et al. (1985).

Morphology.— We measured 18 morphometric characters for 175 of the specimens (Appendix Table 1). In addition, we examined outgroup specimens of *Phrynobatrachus calcaratus* ($n = 5$), *P. parvulus* ($n = 3$), *P. cornutus* ($n = 8$) and *P. minutus* ($n = 11$). Measurements were taken using Vernier calipers, frequently with the aid of a dissection microscope, to a precision of 0.1 mm. Measurements recorded include: snout-vent length (SVL), head length (HDL), head width (HDW), width of the eye at its widest point (EYE), width of the interorbital space (IOS), width of the internarial space (INS), distance between the eye and the naris (ENS), distance between the naris and the tip of the snout (NS), distance between the naris and the edge of the upper lip (NLL), tibia-fibula length (TiL), femur length (FeL), tarsus length (TaL), distance between the inner and outer metatarsal tubercles (IOMT), distance between the inner and tarsal tubercles (ITT), distance between the tip of the fourth toe and the base of the inner metatarsal tubercle (ToL4), distance between the tip of the first toe and the base of the outer metatarsal tubercle (ToL1), width of the hand at its widest point (HaW) and distance between the base of the hand and the tip of the third

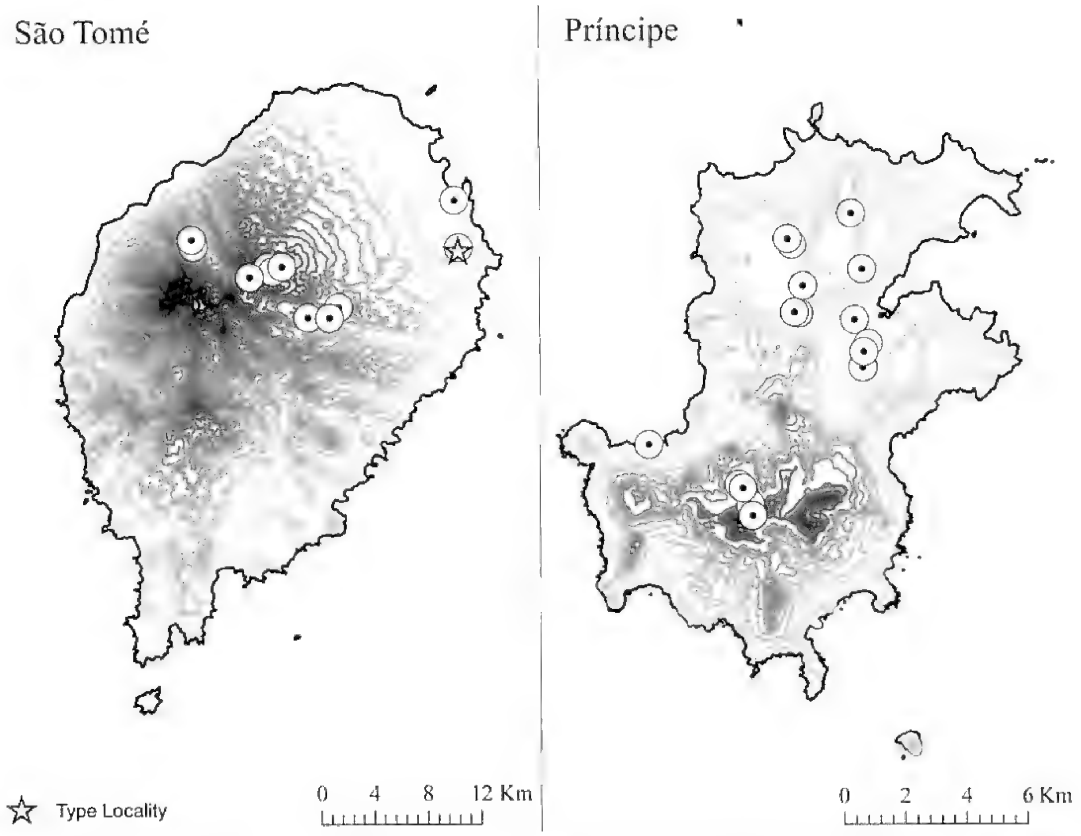

FIGURE 1. Collection localities from Príncipe and São Tomé. Type locality for *P. leveleve* on São Tomé is indicated.

finger (FiL3). We performed linear discriminant function analysis (DFA) of males for *P. dispar* and *P. leveleve* using ratios of 17 morphometric characters to SVL. For each island population, we randomly divided individuals into equal subgroups, only one of which was used to calculate the discriminant functions. The remaining individuals, as well as the two syntypes of *P. feae,* were reclassified using the discriminant function to determine reclassification scores.

OSTEOLOGY.— Two males and one female from each island were cleared and double-stained with alcian blue and alizarin red dyes, following the procedure of Dingerkuis and Uhler (1977), as modified by Drewes (1984). Specimens were examined using a dissecting microscope.

CYTOCHROME B SEQUENCES.— We extracted mitochondrial DNA from 17 ingroup specimens and one outgroup specimen (*Phrynobatrachus dendrobates,* Appendix Table 2) using a Qiagen DNeasy tissue extraction kit (Qiagen Inc, Valencia, CA, USA) following the manufacturer's recommendations for animal tissue. Cytochrome b sequences were amplified using the L-strand primer MVZ15 [5' GAA CTA ATG GCC CAC ACW WTA CGN AA 3'] (Moritz et al. 1992) and the H-strand primer Ptacek2-H [5' TCT TCT ACT GGT TGT CCT CCG ATT CA 3'] (Appendix Table 3, Ptacek et al. 1994). We performed hot start PCR reactions using 100 µL volumes with the top mix and bottom mix initially separated with a wax bead. The top mix (25 µL) consisted of 16 µL ddH_2O, 5 µL 10X Promega thermocycle buffer, 2 µL 10 mM dNTP, and 1 µL 25 µM of each primer. Bottom mix (75 µL) consisted of 0.5–20 µL of extracted DNA, 5 µL 10X Promega thermocycle buffer, 3–5 µL 50 mM $MgCl_2$, 1.5–2.5 µL Bioline Taq DNA Polymerase (Bioline, London, UK) and ddH_2O added to 75 µL. PCR reactions were carried out using a Perkin-Elmer 9600

Cetus PCR thermocycler. PCR product was verified using electrophoresis on a 0.8% agarose gel and staining with Ethidium Bromide. PCR product was purified using the Promega Wizard PCR Preps DNA Purification System (Promega, Madison, WI, USA) according to manufacturer's recommendations. We subsequently cycle sequenced the PCR product (10 µL volumes) using 0.5–4 µL template, 1 µL 2.5 µM primer, 0.5 µL DMSO, 1 µL 5X Promega thermocycle buffer and 1 µL Big Dye v.3.1 reaction premix (Perkin-Elmer, Norwalk, CT, USA) filled to a total volume of 10 µL with ddH_2O. The cycle sequencing product was precipitated and washed with 100% ethanol, denatured with formamide and sequenced using an ABI-Prism 3100 Genetic Analyzer (Applied Biosystems, Foster City, CA, USA).

Forward and reverse complement sequences were edited, aligned and checked visually for ambiguous base assignments using Sequencher 3.0 (Gene Codes Corporation). Sequences were aligned using ClustalX v.1.83 (Thompson et al. 1997). Sequences were protein-coding and thus alignment was unambiguous with no indels. A model of molecular evolution was selected from the data using Modeltest 3.7 using the corrected Akaike Information Criterion (Posada and Crandall 1998). Once a model was selected, the sequences were imported into PAUP* (Swofford 1999) and a maximum-likelihood (ML) tree constructed using a heuristic search with tree-bisection-reconnection (TBR) branch swapping with 10 random addition sequence replicates. Bootstrap support for the resulting nodes was estimated using 1000 ML bootstrap replicates with TBR branch swapping and 10 random addition sequence replicates (Felsenstein 1985). All unique sequences were deposited in Genbank (EUO 74967-984).

12S rRNA, tRNA-valine, and 16S rRNA Sequences.— DNA from 28 specimens (Appendix Table 2) was extracted and the mitochondrial 12S rRNA, valine-tRNA, and 16S rRNA regions were sequenced to obtain a fragment of about 2350 base pairs (Appendix Table 3). The fragment was amplified using four overlapping PCR products of approximately 600bp. Sequences were aligned using ClustalX and further refined utilizing MacClade 4.06. Maximum Parsimony analyses were carried out utilizing PAUP* 4.0b10 (Swofford 2002), using the heuristic search option with TBR branch swapping and 1000 random addition sequence replicates. A model of molecular evolution was selected from the data using Modeltest 3.7 using Hierarchical Likelihood Ration Tests (Posada and Crandall 1998). Once a model was selected, the sequences were imported into PAUP* (Swofford 1999) and a maximum-likelihood (ML) tree constructed using a heuristic search with tree-bisection-reconnection (TBR) branch swapping with 10 random addition sequence replicates. Bootstrap support for the resulting nodes was estimated using 100 ML bootstrap replicates with TBR branch swapping and 10 random addition sequence replicates (Felsenstein 1985). All unique sequences were deposited in Genbank (EUO 75275-302).

Species Description

***Phrynobatrachus leveleve* Uyeda, Drewes, and Zimkus, sp. nov.**

Material examined.— Holotype: CAS 218901 male; São Tomé and Príncipe: São Tomé Island, Caxueira, along Agua Pete Pete, 0°18′N, 6°44′E, elevation 50 m. Collected by R.C. Drewes, R.E. Stoelting, and J.V. Vindum, 5 April 2001. Paratypes: CAS 218894, CAS 218892 male and female respectively and CAS 218895 (male, cleared and stained) collected from type locality (sequences from this specimen are also included in Frost et al., 2006). CAS 219003 male and CAS 218998 (female, cleared and stained), collected from Java 0°16′N, 6°39′E, elevation 600 m. CAS 219066 female; collected from the west side of the Rio Contador, 0°18′N, 6°33′E, elevation 700 m. All specimens collected between 2–15 April 2001 by R.C. Drewes, R.E. Stoelting, and J.V. Vindum. Other Material Examined: CAS 218893 female; CAS 218896–218900 males; from type locality. CAS 218906 male; on road between Bombaim and Santa Adelaide at Rio Abade bridge

0°15′N, 6°38′E, elevation 50 m. CAS 218918, 218919, 219064, 219065 females; CAS 219067 male; on west side of the Rio Contador, 0°18′N, 6°33′E, elevation 700 m. CAS 219406 female, CAS 218995–218997, 218999–219004, 219407–219409 males; Java, 0°16′N, 6°39′E, elevation 600 m. CAS 219027 male; Quisinda, 0°18′N, 6°44′E, elevation 50 m. CAS 219051 female; CAS 219052,219053 males; between Bom Successo and Lagoa Amelia, 0°17′N, 6°36′E, elevation 1100 m. CAS 219264–219268 males; city of São Tomé, 0°20′N, 6°43′E, elevation 0 m. CAS 219319–219321, males; Macambrara, 0°17′N, 6°36′E, elevation 1100 m. CAS 233677, 233680, 233685, 233688, 233698–233699 females; CAS 233678–233679, 233681–233684, 233686–233687, 233689–233691, 233704 males; vicinity of Abade, (0°20′N, 6°44′E), elevation 400 m. CAS 233700, juvenile; CAS 233701 female; Lagoa Amelia, (0°17′N, 6°35′E), elevation 1412 m.

Diagnosis.— Adult males distinguished from *Phrynobatrachus dispar* by a lower jaw distinctly marked with vertical banding, a darkened vocal sac, the presence of minute spicules arranged in a U-shaped pattern along the anterior margin of the jaw and a proportionally smaller eye (Figs. 2, 3). Dorsal asperities are never as distinct or extensive as those in male *P. dispar* (this difference is obvious even in subadult and recently metamorphosed specimens). Female *P. leveleve* are distinguished from female *P. dispar* by the absence of asperities in most individuals, smaller size and duller coloration (Fig. 4). Although highly polymorphic, the overall coloration of both male and female *P. leveleve* is duller, generally lacking distinct vertical barring on the thigh and leg as found in *P. dispar* (Fig. 2).

Phrynobatrachus leveleve is distinguished from *P. calcaratus* and *P. cornutus* by the absence of an eyelid cornicle (although a small bump may be observed in the same location). *P. leveleve* is further distinguished from *P. parvulus* and *P. minutus* of the mainland by larger size, stouter habitus and smaller femoral glands in males.

Etymology.— The specific epithet is derived from the native Portuguese Creole spoken in the Republic of São Tomé and Príncipe. The phrase, "*leve leve*," generally meaning "easy, easy" or "lightly lightly" has also been translated by Henrique Pinto da Costa, former Minister of Agriculture, as "calmly, surely." In our opinion, all three definitions describe the delightful, easy-going demeanor of the citizens of the Republic São Tomé and Príncipe. With the recent discovery of oil in the Gulf of Guinea, greed and exploitation threaten to disrupt the peaceful culture of São Tomé, and it is with the hope that the citizens of this tiny African nation will maintain their ecological heritage and cheerful outlook on life that we name this diminutive endemic anuran.

Description of the Holotype.— CAS 218901 Male, 15.5mm SVL; total length of the leg is 1.5–2.0 times the SVL. Width of the head greater than 2.5 times the diameter of the eye. Dorsal asperities are indistinct to the naked eye and are most numerous between the posterior half of the eyelid and the tibio-fibula. However, a few asperities extend beneath the eye and onto the snout as well as the anterior portion of the eyelid. Tympanum indistinct, less than half the width of the eye. Two indistinct glandular ridges topped with 3 to 4 white-pointed asperities forming a broken X-shaped pattern are located on the mid-dorsum.

The gular sac is darkened and appears as an inverted "U" shaped patch on the throat. The anterior border of the dark pigment contains numerous spicules that extend from the very tip of the lower jaw posterior to the corners of the mouth. These are found in 5–7 rows on the tip of the jaw and narrow to only 1–2 rows at the angle of the jaw. The medial lingual papilla on the tongue is present. Femoral glands, although indistinct, are present in the middle of the thigh; the glands extend about one-fourth the total length of the thigh.

Webbing between fingers absent, webbing between toes reduced and deeply incised, existing mostly as a narrow fringe on the sides of the toes, webbing formula I2-3II3$^-$–3$^+$III3$^+$-4$^+$IV5$^-$–4$^-$V (Savage and Heyer 1997). Distal phalanx T-shaped, resulting in the appearance of dilated toe tips.

Color in preservative.: Dorsum ground color a dark grayish-brown, lacking many distinctive markings. Two dark blotches over the front legs extend diagonally toward the eye. Faint light inter-

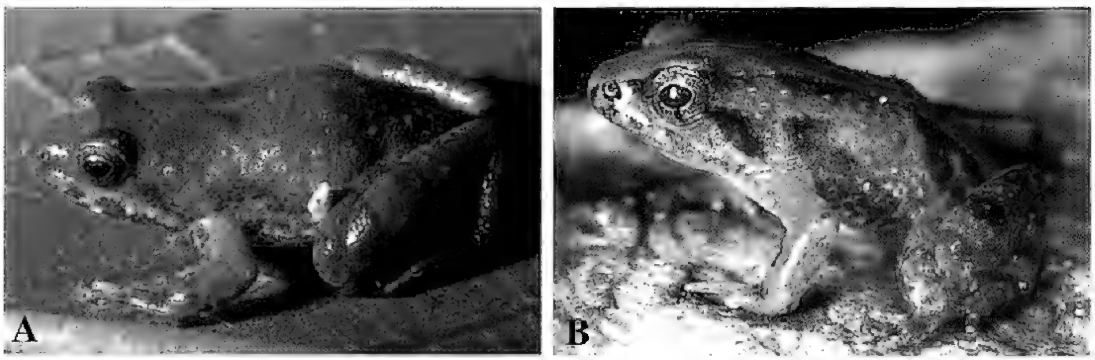

FIGURE 2. Comparison of adult males in life. *P. leveleve* (A.; from series CAS 218995-218003- Java) and *P. dispar* (B.; from series CAS 219080-219124 – Agua Doutor). Notice the more prominent and numerous asperities in *P. dispar* as well as the more striking coloration. Some dark barring on the lower jaw of *P. leveleve* is also visible.

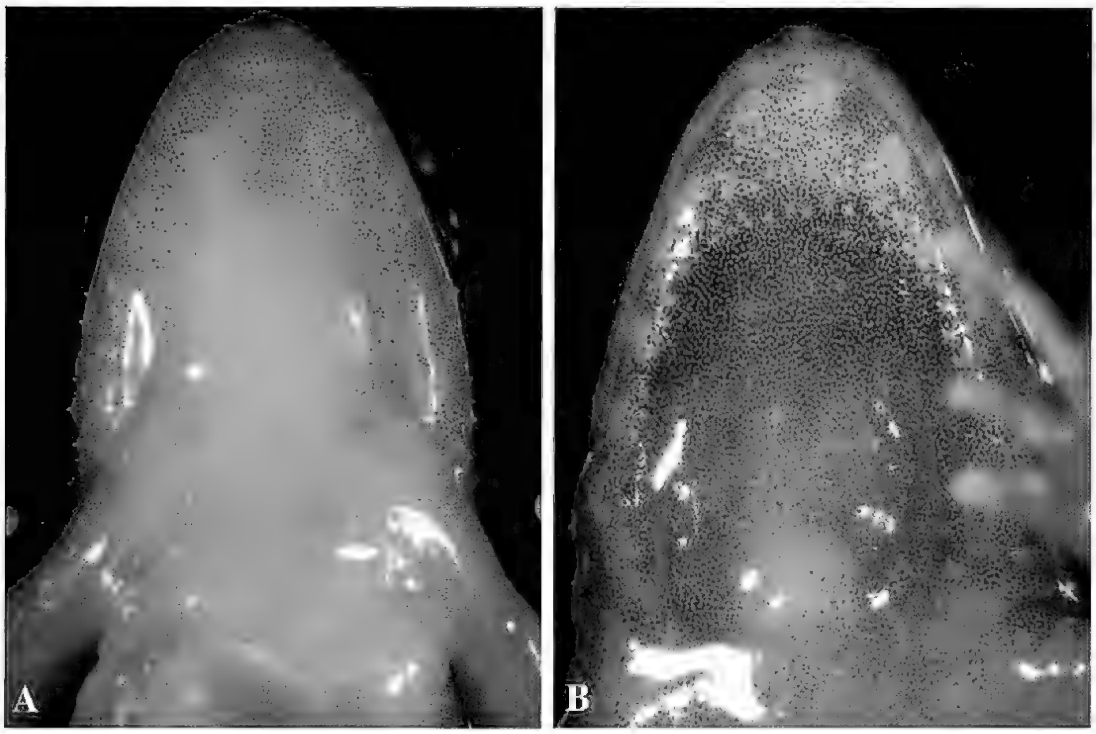

FIGURE 3. Comparison of the throat patterns in *P. dispar* (A) and *P. leveleve* (B). Note the presence of numerous spicules, darkened vocal sac and barring on the lower jaw of *P. leveleve* compared with the clear, cream colored throat of *P. dispar.*

orbital stripe followed by a faint dark patch in the center of the dorsum behind the eyes. Indistinct dark splotches are present on the dorsum. Only one or two faint dark bars are found on either the thigh or the tibio-fibula of the hind limb. Ventrum pale cream-colored and clear except for the throat and a few darkly pigmented spots extending along the flanks to just beyond the front legs. Seven distinct dark brown bars line the lower jaw. Undersides of the hind limbs clear, slight yellowish hue.

VARIATION IN THE PARATYPES.— Morphology of the paratypes is generally consistent with that of the holotype. CAS 218894 male: 14.5 mm SVL, specimen with a dark brown ground and a light mid-dorsal stripe present, approximately 0.2 mm wide, running from just anterior the eyes, split-

ting just before the cloaca into two stripes that run down the posterior side of the both thighs and tibio-fibulae ending at the tarsus. CAS 219003 male: 17.1 mm SVL, lighter brown ground color with distinct darker brown streaks in a broken "X" on the dorsum, above the forelimbs and underneath the tympanum. Dorsal asperities extend onto the snout and hind legs. CAS 219882 gravid female: 18.9 mm SVL, specimen is uniform brown with a grayish wash on the flanks. Ventrum cream colored, only a few flecks of brown, with strong barring on the lower lip. CAS 219066 gravid female: 20.5 mm SVL, specimen is uniform brown with a dark snout. Ventral surface marked with large dark splotches throughout.

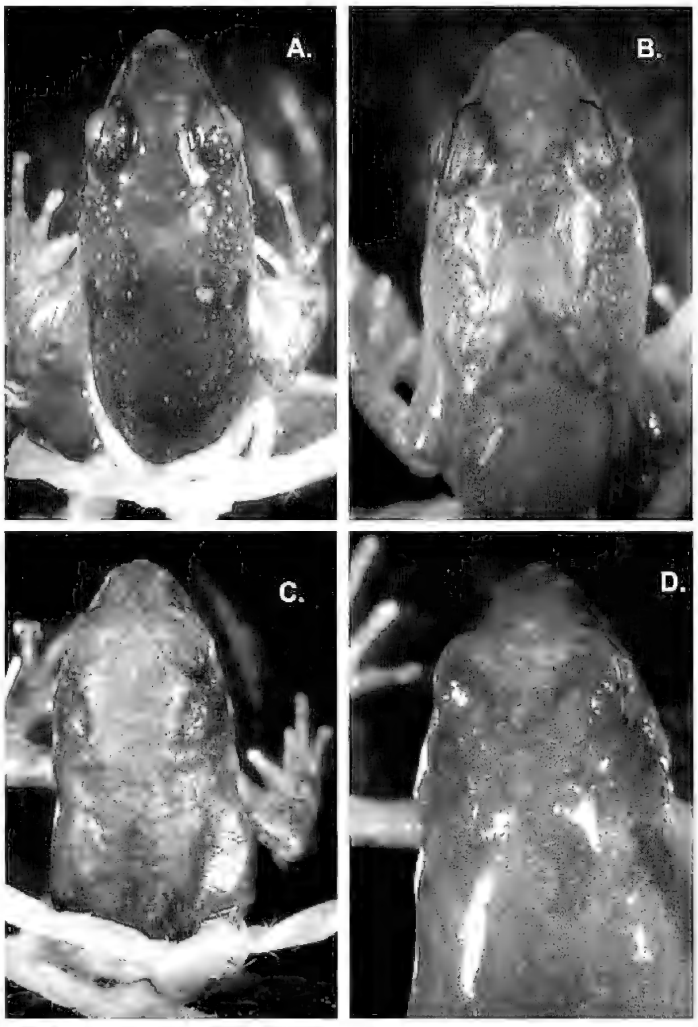

FIGURE 4. Comparison of dorsal asperities in *P. dispar* male (A) and female (C) with *P. leveleve* male (B) and female (D).

CYTOCHROME B SEQUENCE VARIATION.— We obtained sequences for seven individuals from four localities on Príncipe and eight individuals from three localities on São Tomé (Appendix Table 2). Outgroup sequences include a single sequence obtained for *P. dendrobates* as well as two sequences obtained from Genbank: *Rana catesbeiana* (AF205089) and *Rana nigromaculata* (AY315755). A segment of the cytochrome b gene 776 bp long was obtained for all individuals included in the analysis. Base frequencies were typical of vertebrate mitochondrial sequences [f(A) = 0.24, f(C) = 0.31, f(G) = 0.14, f(T) = 0.31]. Among ingroup taxa, there were 150 variable sites, 136 of which were parsimony informative. Modeltest selected a TVM+I+G model with a gamma distribution of 3.2151 and a proportion of invariable sites of 0.5128.

Intra-island pairwise comparisons were generally quite low. On Príncipe, sequence divergence ranged from 0.001–0.023 (mean = 0.010 ± 0.002) and on São Tomé, from 0.000–0.009 (mean = 0.004 ± 0.001). By contrast, inter-island pairwise comparisons were quite high, with a mean sequence divergence of 0.21 ± 0.02.

Phylogenetic reconstruction demonstrates monophyly of both *Phrynobatrachus dispar* from Príncipe and *P. leveleve* from São Tomé (Fig. 5). Intra-island sequence divergence was higher on Príncipe than on São Tomé. One individual from Príncipe, CAS 219202, shared 6 bases with São

Tomé sequences that were not found in any other frogs from Príncipe. In fact, no other frog from Príncipe shares more than one parsimony informative site with São Tomé frogs. This likely represents a plesiomorphic state (in CAS 219202), as 4 of 6 these sites share the same base as at least one of the outgroup taxa.

Bootstrap values were high supporting the monophyly of the two island clades apart from *P. dendrobates*. In addition, there are high bootstrap values for both island clades, although there is a considerably lower value for the Príncipe clade (bootstrap value = 76). This decreased value is again due to CAS 219202, which shares character states with São Tomé populations to the exclusion of the rest of the Príncipe clade. Furthermore, for *P. leveleve* to be nested within *P. dispar* it would require an unrealistic disparity in rates of mutation. In fact, the bootstrap value becomes 100 when a molecular clock is enforced.

12S rRNA, valine-tRNA, and 16S rRNA sequence variation.— Approximately 2.4 kb of mtDNA, including the12S rRNA, valine-tRNA, and 16S rRNA genes, was obtained for 28 individuals representing twelve species of *Phrynobatrachus* (Appendix Table 2). *Petropedetes newtoni* (MCZ136798) was included as the outgroup for this particular analysis. The maximum parsimony (MP) strict consensus and maximum likelihood (ML) tree resulted in fully compatible topologies. The MP analysis of 2,456 characters (960 variable, 762 parsimony informative) yielded one most parsimonious tree (Fig. 6). Base frequencies were typical of vertebrate mitochondrial sequences [f(A) = 0.34, f(C) = 0.23, f(G) = 0.18, f(T) = 0.25]. Modeltest selected a TrN+I+G model with a gamma distribution of 0.4126 and a proportion of invariable sites of 0.2794.

Phylogenetic reconstruction utilizing the12S rRNA, valine-tRNA, and 16S rRNA genes demonstrates monophyly of both *Phrynobatrachus dispar* from Príncipe and *P. leveleve* from São Tomé. Sequence divergence within species was generally trivial compared to among-species divergences with inter-island pair-wise comparisons having a mean sequence divergence of 0.057 ± 0.002. Intra-island sequence divergence was slightly higher on Príncipe than on São Tomé. Sequence divergence of *Phrynobatrachus* from Príncipe ranged from 0.001–0.005 (mean = 0.003 ± 0.001), whereas on São Tomé the divergence ranged from 0.001–0.003 (mean = 0.002 ± 0.001) (Fig. 6).

There are high ML bootstrap values for each island clade, supporting the monophyly of both *Phrynobatrachus dispar* and *P. leveleve*. In addition, bootstrap values of the clade containing these two sister species were high, supporting the two island species apart from other East African *Phrynobtrachus*. Lastly, the monophyletic group including *Phrynobatrachus dispar*, P. *leveleve*, and a group of East African species (*P. keniensis*, *P. inexpectatus*, *P. cf. minutus*, *P. parvulus*, and *P. rungwensis*) was found have high bootstrap values (Figs. 5, 6).

Morphological Variation.— Intra-island variation: Both *Phrynobatrachus dispar* and *P. leveleve* exhibit strong sexual dimorphism. Male *P. dispar* are distinguished by greater density and size of dorsal asperities, smaller size and the presence of nuptial pads. Female *P. dispar* also have dorsal asperities, but these are much smaller, more numerous, and located predominantly on the flanks. In *P. leveleve*, males have small and sparsely distributed dorsal asperities, a darkened vocal sac and small spicules on the underside of the throat. Most female *P. leveleve* lack dorsal asperities entirely, and extremely small and sparse asperities were only observed in a single individual (CAS 233677).

In general, within island morphology was consistent on both São Tomé and Príncipe. Furthermore, we found no evidence for the bimodal distribution of tubercle distance ratios (ITT/IOMT) that Boulenger used to distinguish *Phrynobatrachus feae*. This measurement often varied in a single individual, depending on whether the right or left foot was used. Although larger individuals were often found at higher elevations, this variation appears to be continuous rather than discrete

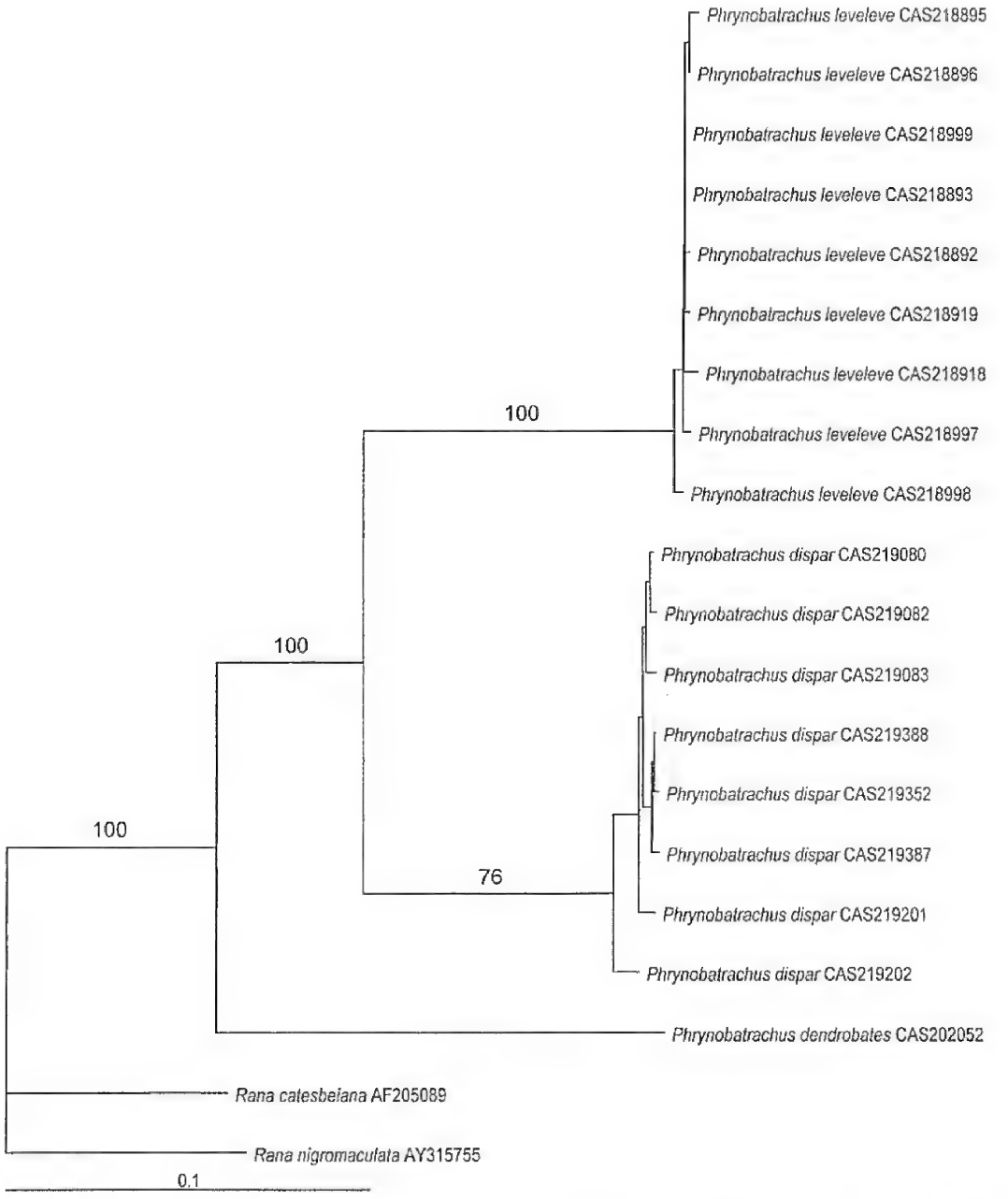

FIGURE 5. Maximum likelihood phylogram of cytochrome b gene with bootstrap support indicated at the nodes. Note the large sequence divergence between *P. dispar* from Príncipe and *P. leveleve* from São Tomé.

(Fig. 7). Thus, it appears that Baillie's observation that two distinct size classes in different habitats may have actually been an observation of Bergmann's rule across an elevational gradient (Ashton 2002). Both São Tomé and Príncipe rise steeply out of the ocean, and it is easy to imagine mistaking continuous variation based upon elevation for discrete size classes. Interestingly, this phenomenon has also been observed in the island's endemic caecilian, *Schistometopum thomense*,

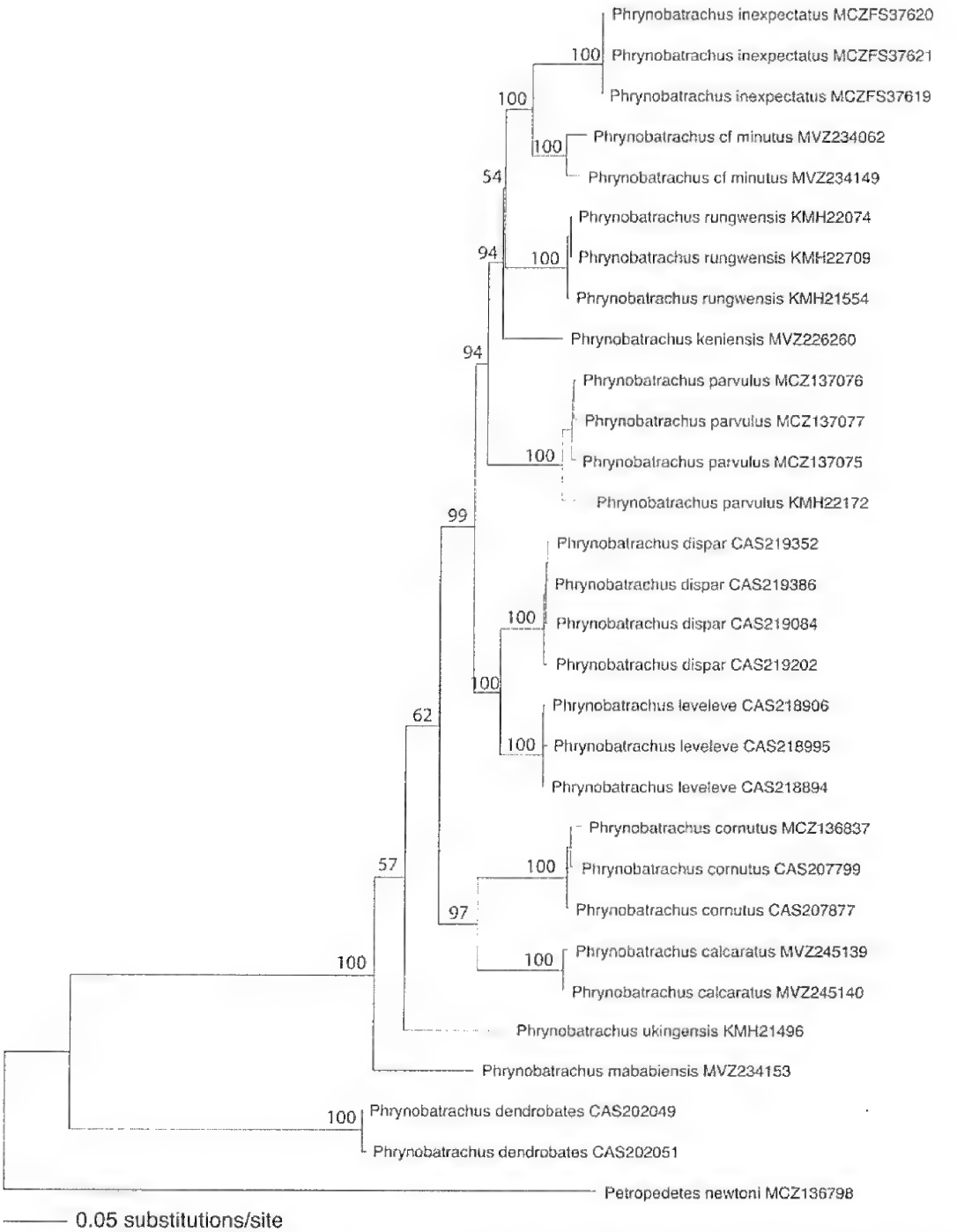

FIGURE 6. Maximum likelihood phylogeny of combined 12S rRNA, valine t-RNA, and 16S rRNA of 12 species of *Phrynobatrachus*. Bootstrap values are indicated at the nodes.

which reaches its greatest size at higher elevations (Measey and Van Dongen 2006).

INTER-ISLAND VARIATION: *Phrynobatrachus dispar* and *P. leveleve* can be readily distinguished from each other in both sexes. Males of *P. leveleve* have fewer asperities, which are only faintly noticeable to the naked eye. By contrast, *P. dispar* males have distinct white-tipped conical asperities (Figs. 2 and 3). Consistent with Baillie's observation (1999) that there are more color morphs on Príncipe than on São Tomé, the dorsal coloration of *P. dispar* is more striking than that of *P. leveleve*, which is most often a drab grayish brown in alcohol. Dark barring on the legs is also more distinct in *P. dispar* than *P. leveleve* (Fig. 2). Ventral coloration follows the opposite pattern. Male *P. dispar* usually have a clear, cream colored throat whereas male *P. leveleve* have dark barring on the lower jaw, a darkened vocal sac and minute spicules along its anterior margin. As noted by Frost et al (2006), the presence of spicules on the throat appears sporadically within the Phrynobatrachidae and Petropedetidae, in taxa as morphologically divergent as *Conraua* and *Phrynobatrachus*, yet may be absent in a sister species as observed in the Gulf of Guinea *Phrynobatrachus*.

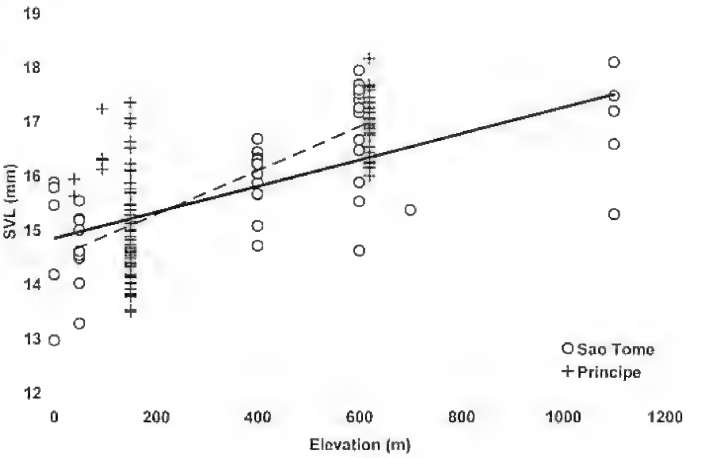

FIGURE 7. Increasing snout-vent length (SVL) with increasing elevation for adult males from Príncipe and São Tomé. Solid line is the regression line for São Tomé, dashed line is for Principe. Regression lines for both islands have highly significant non-zero slopes ($p < 0.01$).

Female *Phrynobatrachus dispar* are distinguished from female *P. leveleve* by the presence of numerous minute asperities on the flanks of the body (Fig. 4). Ventral coloration varies from large, distinct brown blotches against a cream colored background to diffuse mottling of light brown spots and various combinations thereof. Individuals of both species exhibit varying degrees of dark barring on the lower jaw.

The two species are remarkably similar morphometrically given the high values obtained for sequence divergence (Appendix Table 4). Females from Príncipe were significantly larger ($N = 20$, mean SVL = 22.2 mm) than females from São Tomé ($N = 17$, SVL = 19.6), even though females from São Tomé were collected, on average, at higher elevations than individuals from Príncipe. For inter-island comparisons between males, EYE, ENS, HaW, NLL, and FiL3 differed significantly (2-tailed student's t-test, $p < 0.05$), as well as the ratios in both sexes for EYE/NLL (males and females, $p < 0.01$), EYE/HW (males, $p < 0.01$; females, $p < 0.05$) and HaW/FiL3 (males and females, $p < 0.01$) (Appendix Table 4). In particular, the size of the eye in *P. dispar* is noticeably larger than in *P. leveleve*. Although there is some overlap in this character, the maximum measurement in *Phrynobatrachus leveleve* is less than the mean for *P. dispar* in both males and females.

Discriminant function analysis indicated reliable patterns of character variation for males of the ingroup taxa, although some overlap did occur. A second DFA using only a random subset of each of the ingroup species weighted loadings similarly to the first, with the highest absolute loadings for the ratios of EYE, NLL, and ENS to SVL. Furthermore, of those individuals that were not included in the smaller sample DFA, 86% of *Phrynobatrachus dispar* ($N = 26$) and 81% of *P. leveleve* ($N = 16$) were correctly identified to species. Classification of the two *P. feae* type specimens

examined was split, with one being classified as *P. dispar* and one being classified as *P. leveleve* by the discriminant functions. This is not surprising inasmuch as the data used to train the discriminant functions are based primarily on measurements of adults, whereas the types of *P. feae* appear to be juveniles. Combined with the morphological homogeneity and low sequence divergence values for intra-island comparisons, we conclude that *P. feae* is a junior synonym of *P. dispar*.

Internal morphology is similar in all six individuals examined, suggesting that these two species are closely related. Some differences in skull morphology were observed between *Phrynobatrachus dispar* and *P. leveleve*. The anterior margin of the frontoparietal in *P. dispar* is deeply incised, whereas in *P. leveleve* it is only slightly irregular, and the spacing between the nasal cartilage appears greater in *P. dispar* than in *P. leveleve* (Fig. 8), although this character was variable in our small sample size.

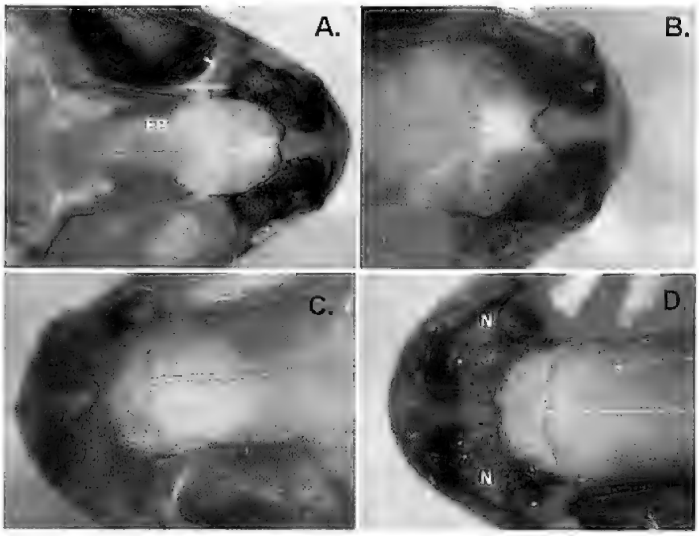

FIGURE 8. Snout of cleared and double-stained specimens of *P. dispar* male (A), female (B), and *P. leveleve* male (C) and female (D). Notice the anterior margin of the frontoparietal (FP) in *P. dispar* is more deeply incised than that of *P. leveleve*. Also the spacing between the nasals (N) is greater in the former.

DISCUSSION

Although we find no evidence for the existence of two taxa on Príncipe, it is intriguing that Boulenger describes *Phrynobatrachus feae* as having a throat that is dark brown or black, with uniform or round white spots (Boulenger 1906), which is a character we use to distinguish *P. leveleve*. All adult material we examined from Príncipe possessed a clear white throat. It is possible that Boulenger's specimens, collected by L. Fea, may have been from São Tomé, but there are no existing records at the British Museum that suggest the specimens were collected elsewhere than Príncipe ("Prince's Island") (B.T. Clarke, pers. comm.). Furthermore, the syntypes of *P. feae* examined (BMNH 1947.2.6.89, 91) appear to be juvenile *P. dispar*. Juvenile specimens tend to be darker overall and often have completely dark throats that fade at maturity. Although the coloration and presence of asperities on the syntypes were difficult to determine because of their state of preservation, we could find no reason to doubt that these are juvenile *P. dispar* collected from Príncipe Island.

Sequence data demonstrates considerable divergence between the two island species of *Phrynobatrachus*. Using a low estimate of divergence of 19% for the cytochrome b gene and a molecular clock estimate as high as 1.4% sequence divergence per million years, a value considerably higher than estimated divergence rates found in other amphibians (Caccone et al. 1997; Veith et al. 2003), suggests a time of divergence that predates the estimated origin for São Tomé of 13 million years ago (Lee et al. 1994). This would seem to suggest that the most likely scenario for the divergence of the two species would be independent colonizations from mainland Africa. After the recognition into two *Phrynobatrachus* species, each endemic to a single island, only one species of amphibian, *Hyperolius molleri*, appears to have successfully dispersed from one island to the other (or recently colonized both islands). However, it is difficult to make conclusions with

any certainty given the unreliability of molecular clock estimates, the uncertainty of the sequence divergence, and the possibility that the estimated age of São Tomé may actually be much greater than 13 million years (orogeny dates were based upon the oldest lava flows, which only set a minimum age for the island). Analyses of 12S rRNA, valine-tRNA, and 16S rRNA mtDNA further support the divergence between the two island species of *Phrynobatrachus* as intra-island variability was low in comparison to interspecific divergence.

Surprisingly, a number of recent molecular studies suggest that many of the endemic amphibians of the Gulf of Guinea islands may be more closely related to East African species than to their West African congeners; these studies include the fossorial caecilian, *Schistometopum thomense* (Wilkinson et al. 2003), *Ptychadena newtoni* (Measey et al. 2007) and, perhaps the treefrogs, *Hyperolius molleri* and *H. thomensis*. (Drewes and Wilkinson 2004, show the closest outgroup relative to be *H. cinnamomeoventris*, whose range includes East Africa). Similar claims have been made for the endemic terrestrial gastropod mollusk, *Bocageia* (Gascoigne 1994). Whereas this pattern may be a reflection of poor sampling in the intervening Congo Basin, the inclusion of the larger dataset (BMZ) in this study (12 *Phrynobatrachus* species) seems to support a Gulf of Guinea island-East Africa relationship (Fig. 6). *Phrynobatrachus dispar* and *P. leveleve* consistently form a clade with *Phrynobatrachus* species from Ethiopia, Kenya, Malawi, and Tanzania (*P. keniensis*, *P. inexpectatus*, *P.* cf. *minutus*, *P. parvulus*, and *P. rungwensis*), rather than with the West African species *P. calcaratus* and *P. cornutus*. This curious pattern draws attention to the need for phylogenetic reconstruction of the Gulf of Guinea amphibians within the context of the African amphibian fauna, which may provide considerable data on the mechanisms and timing of colonization events. Currently such studies are limited by poor collections across Africa, especially the Congo Basin, and a paucity of researchers with an interest in African herpetofauna. We call attention to this deficit in the hopes that future researchers will take on the challenge of providing a comprehensive treatment of these species.

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Appendix

TABLE 1. Localities for all specimens for which morphological data were collected. Additional information is available online in the CAS catalog: *<http://www.calacademy.org/research/herpetology/catalog/>*

Species	Catalog Number	Elev.	Locality	Lat. and Long.
P. leveleve	CAS 218892-6218901	50 m	São Tomé	0°18′N, 6°44′E
	CAS 218906	50 m		0°15′N, 6°38′E
	CAS 218918-218919, 219064-219067	700 m		0°18′N, 6°33′E
	CAS 218995-219003, 219406-219409, 219004	600 m		0°16′N, 6°39′E
	CAS 219027	50 m		0°18′N, 6°44′E
	CAS 219051-219053	1100 m		0°17′N, 6°36′E
	CAS 219264-219269	0 m		0°20′N, 6°43′E
	CAS 219319-219321	1100 m		0°17′N, 6°36′E
	CAS 233677-233691, 233704	400 m		
	CAS 233700-233701	1412 m		
P. dispar	CAS 219080-219124	150 m	Príncipe	1°39′N, 7°25′E
	CAS 219143-219147	150 m		1°40′N, 7°25′E
	CAS 219201-219202	0 m		1°36′N, 7°21′E
	CAS 219211	0 m		
	CAS 219345-219346	175 m		1°39′N, 7°24′E
	CAS 219352-219356	150 m		1°38′N, 7°24′E
	CAS 219363	50 m		1°38′N, 7°25′E
	CAS 219385-219392, 233535-233567	620 m		1°35′N, 7°23′E
	CAS 219393-219394, 233569	948 m		1°34′N, 7°23′E
	CAS 233527-233530, 233533-233534	40-95 m		
"*P. feae*"	BMNH.1947.2.6.89, 91*		Príncipe	
P. cornutus	CAS 207877-207880, 207885, 207890, 207897-207901		Bioko Id	3°19′N, 8°40′E
P. calcaratus	CAS 199267-199299		Cameroon	3°11′N, 12°49′E
P. parvulus	CAS 204580-204592		Uganda	
P. cf. *minutus*	CAS 122939-122964		Marsabit, Kenya	

* Syntypes

TABLE 2. Specimens included in the two molecular datasets.

Species	Collection no.	Locality	Genbank acc#
16S rRNA, 12S rRNA and tRNA Valine			
Phrynobatrachus dispar	CAS219084	Príncipe	EU075275
	CAS219202	Príncipe	EU075276
	CAS219352	Príncipe	EU075277
	CAS219386	Príncipe	EU075278
P. leveleve	CAS218894*	São Tomé	EU075279
	CAS218906	São Tomé	EU075280
	CAS218995*	São Tomé	DQ283223
P. calcaratus	MVZ245139	Ghana	EU075281
	MVZ245140	Ghana	EU075282
P. cornutus	CAS207799	Bioko	EU075283
	CAS207877	Bioko	EU075284
	MCZ136837	Cameroon	EU075285
P. dendrobates	CAS202049	Uganda	EU075286
	CAS202051	Uganda	EU075287
P. cf. minutus	MVZ234062	Kenya	EU075288
	MVZ234149	Kenya	EU075289
P. inexpectatus	MCZFS37619	Ethiopia	EU075290
	MCZFS37620	Ethiopia	EU075291
	MCZFS37621	Ethiopia	EU075292
P. keniensis	MVZ226260	Kenya	EU075293
P. mababiensis	MVZ234153	Kenya	EU075294
P. parvulus	MCZ137075	Malawi	EU075295
	MCZ137076	Malawi	EU075296
	MCZ137077	Malawi	EU075297
P. rungwensis	KMH21554	Tanzania	EU075298
	KMH22074	Tanzania	EU075299
	KMH22709	Tanzania	EU075300
P. ukingensis	KMH21496	Tanzania	EU075301
Petropedetes newtoni	MCZ136798	Cameroon	EU075302
Cytochrome b			
Phrynobatrachus dispar	CAS219201	Príncipe	EU074967
	CAS219202	Príncipe	EU074974
	CAS219080	Príncipe	EU074968
	CAS219082	Príncipe	EU074969
	CAS219083	Príncipe	EU074973
	CAS219352	Príncipe	EU074972
	CAS219387	Príncipe	EU074970
	CAS219388	Príncipe	EU074971
P. leveleve	CAS218997	São Tomé	EU074980
	CAS218998*	São Tomé	EU074977
	CAS218999	São Tomé	EU074978
	CAS218918	São Tomé	EU074983
	CAS218919	São Tomé	EU074979
	CAS218892	São Tomé	EU074976
	CAS218893	São Tomé	EU074982
	CAS218895	São Tomé	EU074975
	CAS218896	São Tomé	EU074981
P. dendrobates	CAS202052	Uganda	EU074984
Rana catesbeiana		USA	AF205089
R. nigromaculata		Korea	AY315755

Paratypes *

TABLE 3. Primers used to amplify cytochrome b, 12S rRNA, tRNA valine, and 16S rRNA genes

Primer Name	Designation (1)	Position*
MVZ15-L	141 MVZ15-L	16243-16268
Ptacek2-H	168 Ptacek2-H	17257-17282
MVZ59-L	29 MVZ59	2153-2180
MVZ59B-L	————	2236-2263
12L1-L	46 L1091	2475-2509
12SM-L	————	2968-2988
tRNAval-H	73 tRNAval-H	3034-3059
16SH-H	————	3282-3304
16SC-L	————	3623-3642
16SA-H	88 16Sar-H	3956-3975
16SD-H	96 16Sbr-H	4549-4574

*Positions relative to *Xenopus laevis* mitochondrial genome 1. Goebel, A.M., et al. 1999. *Molecular Phylogenetics and Evolution* 11(1):163-199.

TABLE 4. Male and female morphometric data for all adult ingroup specimens examined. Significant values t-test values for both interisland, same sex comparisons are indicated by an asterisk (*) (two-tailed, $p < 0.05$). See methods for abbreviations. Measurements: Range; mean ± S.D.

	P. dispar males (*n*=84)	*P. dispar* females (*n*=20)	*P. leveleve* males (*n*=44)	*P. leveleve* females (*n*=17)
SVL	13.5-18.1; 15.6 ± 1.3	17.8-24.7; 22.2 ± 1.9	13.0-18.1; 15.8 ± 1.2	18.1-21.4; 19.6 ± 1.0
HDL	5.9-8.1; 6.8 ± 0.5	7.1-10.1; 9.3 ± 0.8	5.8-8.0; 6.8 ± 0.5	7.3-8.5; 8.1 ± 0.4
HDW	4.8-6.4; 5.6 ± 0.4	6.2-9.1; 8.1 ± 0.7	4.5-6.2; 5.5 ± 0.4	6.1-7.5; 6.7 ± 0.4
EYE*	1.9-2.7; 2.3 ± 0.2	2.4-3.5; 3.0 ± 0.3	1.8-2.3; 2.0 ± 0.1	2.2-2.8; 2.4 ± 0.1
IOS	1.4-2.1; 1.8 ± 0.2	1.8-3.0; 2.4 ± 0.2	1.2-2.1; 1.7 ± 0.2	1.4-2.4; 2.1 ± 0.3
INS	1.7-2.2; 1.9 ± 0.1	2.1-3.0; 2.6 ± 0.2	1.6-2.2; 1.9 ± 0.2	1.9-2.5; 2.2 ± 0.1
ENS*	1.3-1.8; 1.5 ± 0.1	1.4-2.5; 2.0 ± 0.2	1.0-1.6; 1.3 ± 0.1	1.1-1.9; 1.7 ± 0.2
NS	0.9-1.5; 1.1 ± 0.1	1.1-1.9; 1.6 ± 0.2	0.6-1.4; 1.1 ± 0.1	1.2-1.6; 1.3 ± 0.1
NLL*	0.8-1.3; 1.0 ± 0.1	1.0-1.6; 1.3 ± 0.1	0.8-1.2; 1.0 ± 0.1	1.1-1.4; 1.2 ± 0.1
TiL	7.3-9.8; 8.4 ± 0.6	8.9-13.2; 11.9 ± 1.2	6.6-9.4; 8.3 ± 0.7	8.4-11.3; 10.3 ± 0.7
FeL	7.0-9.3; 8.0 ± 0.6	8.4-12.7; 11.2 ± 1.2	6.0-9.0; 7.7 ± 0.7	8.1-10.8; 9.7 ± 0.8
TaL	4.1-5.6; 4.7 ± 0.3	4.9-7.1; 6.5 ± 0.6	3.7-5.3; 4.6 ± 0.4	4.6-6.4; 5.7 ± 0.4
IOMT	0.5-0.9; 0.7 ± 0.1	0.7-1.2; 1.0 ± 0.2	0.3-1.0; 0.7 ± 0.2	0.4-1.2; 0.8 ± 0.2
ITT	0.7-1.4; 1.0 ± 0.2	0.9-1.9; 1.4 ± 0.3	0.4-1.2; 0.9 ± 0.2	0.7-1.6; 1.1 ± 0.2
ToL4	7.0-9.6; 8.3 ± 0.6	9.2-13.0; 11.7 ± 1.1	6.3-10.0; 8.3 ± 0.8	8.5-11.6; 10.3 ± 0.8
ToL1	1.8-2.8; 2.2 ± 0.2	2.4-3.8; 3.2 ± 0.4	1.7-2.9; 2.2 ± 0.3	2.2-3.2; 2.8 ± 0.3
HaW*	1.2-2.2, 1.6 ± 0.2	1,5-2.2; 1.9 ± 0.2	1.1-1.8; 1.5 ± 0.2	1.2-1.9; 1.6 ± 0.2
FiL3*	3.1-4.6; 3.9 ± 0.3	4.3-6.1; 5.4 ± 0.5	3.2-4.7; 4.0 ± 0.3	4.3-5.4; 4.8 ± 0.3
ENS/NLL*	1.3-1.8; 1.6 ± 0.1	1.3-1.9; 1.5 ± 0.1	1.1-1.6; 1.3 ± 0.1	0.9-1.6; 1.3 ± 0.1
EYE/NLL*	2.0-2.9; 2.4 ± 0.2	2.1-2.6; 2.3 ± 0.2	1.7-2.4; 2.1 ± 0.2	1.7-2.3; 1.9 ± 0.1
HW/EYE*	2.1-2.8; 2.4 ± 0.1	2.4-3.0; 2.7 ± 0.2	2.4-3.0; 2.7 ± 0.2	2.5-3.1; 2.8 ± 0.2
FiL3/HaW	1.9-3.0; 2.4 ± 0.2	2.5-3.3; 2.9 ± 0.3	2.2-3.7; 2.6 ± 0.3	2.6-3.8; 3.0 ± 0.3
ITT/IOMT	1.0-2.0; 1.4 ± 0.2	1.0-2.1; 1.5 ± 0.3	0.9-2.4; 1.3 ± 0.3	0.8-2.0; 1.4 ± 0.3

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Burmese *Hemidactylus* (Reptilia, Squamata, Gekkonidae): Taxonomic Notes on Tropical Asian *Hemidactylus*

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Five species of the gecko genus *Hemidactylus* are commonly reported from Myanmar (Burma). A sixth gecko, *Cosymbotus platyurus*, has been shown recently to be within the tropical Asian clade of *Hemidactylus* species and is included in that genus here. Not all tropical Asian species were included in that molecular study; thus we provide a preliminary assessment of the taxonomic status of all species in the putative tropical Asian clade, with an emphasis on the species occurring within political confines of Myanmar.

One or more species of *Hemidactylus* geckos occur at most localities inventoried by our Myanmar Herpetological Survey program (1997–2003). With a few exceptions, these geckos are readily assigned to the five species recognized as occurring in Myanmar (Smith 1935): *H. bowringii, H. brookii, H. frenatus, H. garnotii, H. karenorum*. None of these species is uniquely Burmese, although *H. karenorum* has the smallest distribution of the five, occurring in Assam and Myanmar (Smith 1935). The other taxa are more broadly distributed and two (*H. frenatus*, *H. garnotii*) have become global via accidental human transport. A sixth species is added to the Burmese *Hemidactylus* fauna by molecular analysis of Carranza and Arnold (2006) identifying *Cosymbotus platyurus* as a member of the tropical Asian clade.

Among our biodiversity inventories, we occasionally find *Hemidactylus* geckos that do not match comfortably the general characteristics that we use to recognize and differentiate the six "typical" Burmese species. These atypical geckos are not, however, the focus of this report. Rather, we provide a preliminary assessment of taxonomic matters affecting the known species of Burmese *Hemidactylus* arising from the molecular phylogenetic study of Carranza and Arnold (2006; abbreviated henceforth as C&A-06). Before proceeding with that assessment, we offer a brief review of the currently recognized species of Burmese *Hemidactylus*.

Materials and Methods

The morphological data of this report derive solely from Burmese specimens vouchering the regional inventories of the Myanmar Herpetological Survey. The specimens examined are identified in the following section. They represent only a subset of vouchers available and purposefully derive from lowland to mid-elevation sites (< 500 m asl) of the Central Dry Zone southward to and including the Ayeyarwaddy and Sittaung deltas. We recognize that these geographically mixed samples may cloud regional differentiation, but our goal is to provide only preliminary descriptions of

the morphology of Burmese *Hemidactylus*. A limited sample size of 20 to 30 individuals for each species is also compatible with this goal. The maps (Figs. 1–6), however, detail the distribution of all Burmese *Hemidactylus* species in the CAS and USNM collections; the specific identity of these specimens relies heavily on their identification (principally by Htun Win, J. Vindum, or G. Zug) at time of cataloging.

The morphological data include the following characters: MEASUREMENTS: **CrusL**, Crus length; **ForeaL**, Forearm length; **HeadL**, Head length; **JawW,** Jaw width; **SnEye**, Snout-eye length; **SnForel,** Snout-forelimb length; **SVL**, Snout-vent length; **SnW,** Snout width; **TrunkL,** Trunk length. SCALATION: **Chin**, Chin (postmental) scales; **4FingLm,** Fourth finger lamellae (scansors); **4FingDv**, Fourth finger lamellae divided; **4ToeLm**, Fourth toe lamellae; **4ToeDv**, Fourth toe lamellae paired; **Inflab**, Infralabials; **NaInf**, Naris-infralabial contact; **SnS**, Snout scales; **Subcaud,** Subcaudal scales; **Suplab,** Supralabials; **PoreTot,** Total pores. These traits are defined in Caleb and Zug (2007). Statistical analysis performed in SYSAT 11.

The synonymies derive from Wermuth (1965), Zug (1990), Bauer (1994), and Kluge (2002). Kluge's list, as the most recent of the synonymies, established the current recognition of available and valid scientific name for these geckos. Only primary synonyms are given. Type localities are given as in the original description, and all type localities were verified against the original descriptions.

SPECIMENS EXAMINED.— *Hemidactylus bowringii*: Magway Divis., Shwe-Settaw CAS 213598–599, 213603, 213619, 213779, 213782–783, 213835, 213838, 213840, 213845, 213860–861, 213876–878, 213882, 231067; Magway Divis., Shin-Ma-Taung CAS 215841, 215843–844, 215846, 215848; Sagaing Divis., miscellaneous localities - Yinpaungtaing CAS 215392, Khim Aye CAS 215434, 215437, Alaungdaw Kathapa N.P. CAS 215444, 215519, 215646, 215759, 215777, Chatthin W.S. – USNM 520552–056, 537425–426, Pale – CAS 215434, 215437, Sweekawngan village – CAS 232243–244.

Hemidactylus brookii: Mandalay Divis., Mt. Popa CAS 213976, 214040–042, 215829, 231277, 231341–342, 231357, USNM 564914–927; Mandalay Divis., Yin Mar Bin CAS 215297; Sagaing Divis., Alaungdaw Kathapa NP CAS 206650 ,

Hemidactylus frenatus: Magway Divis., Shwe-Settaw WS USNM 564861–862; Sagaing Divis., Alaungdaw Kathapa NP USNM 564889–891, Kabaing USNM564895–896, Chatthin WS USNM 520560–565, 524047–051; Sagaing Divis., Yin Bar Min CAS 215306; Yangon Divis., Yangon USNM 520558–559.

Hemidactylus garnotii: Bago Divis., Dawe USNM 564931–932; Mandalay Divis., Pyin-Oo-Lwin USNM 564933–938, 564940, Mt. Popa USNM 564945; Mon State, Kyaikhtiyo WS USNM 564941; Rakhine State., Gaw USNM 564944; Sagaing Divis., Alaungdaw Kathapa N.P. USNM 564942–943, Chatthin W.S. USNM 537427.

Hemidactylus karenorum: Magway Divis., Shwe-Settaw CAS 213597, 213816–817, 213833, 213836, 213846, 231136, USNM 564946–947; Mandalay Divis., Mt. Popa CAS 210670–671, 214048, 214057–058, 214078–079, 214142, 231308, 231313, 231340, USNM 564949–951.

Hemidactylus platyurus: Chin State, Nat-Ma-Taung CAS 222332; Sagaing Divis., Alaungdaw Kathapa NP CAS 204982–983, 210135, 210152–153, 210284, 210286, 210296–297, 210308, 215559, 215585, 215600, 215679, 210308, 215559, 215585, 215600, 215679, 215734, USNM 564952–954, Htamanthi WS CAS 232192.

SYNOPSIS OF BURMESE *HEMIDACTYLUS*

***Hemidactylus bowringii* (Gray)** Bowring's or Asian smooth gecko

Doryura Bowringii Gray 1845:156. Type locality, syntypes without locality data; restricted to "Hong-kong or neighbourhood" by Smith (1935:99).

Leiurus berdmorei Blythe 1853:646. Type locality, "Mergui" [= Myeik Beik, Tanintharyi Divis., Myanmar].

DESCRIPTION.— Adults 34–51 mm SVL; adult SVL not sexually dimorphic: females average

41.8±4.36 mm SVL (35.6–50.7 mm); male average 39.7±3.95 mm SVL (34.5–49.0 mm). Moderately built, somewhat flattened lizards. Proportions (female – mean, min.-max.; male – same): SnForel/SVL 38, 34–41%; 38, 35–40%; TrunkL/SVL 47, 42–51%; 44, 34–51%; ForeaL/SVL 12, 10–14%; 12, 11–14%; CrusL/SVL 14, 12–16%; 14, 12–15%. Tail length (unregenerated) slightly longer than SVL and equal in females and males. Tail flattened, broader than high (oblong in cross-section), and tapering gradually to thin tip.

Head moderately large and broad, distinct from neck, flattened and conical to obovate in dorsal outline. HeadL/SVL 25, 22–27%; 26, 24–29%; JawW/HeadL 64, 57–72%; 62, 51–69%; SnEye/HeadL 40, 35–43%; 40, 35–45%; SnW/HeadL 7, 4–9%; 6, 4–9%. All digits of fore- and hindfeet with digital pads. Digital pads oblong in shape with distal end only slightly wider than proximal end; slender terminal portion (ultimate and penultimate phalanges) of digit arising from within and free of digital pad of all digits. Claws on all digits; slight or no webbing at base of digits.

Head, body, and tail scalation of small, equal-sized, juxtaposed tubercles dorsally and laterally; ventrally slightly overlapping scales, >5× dorsal tubercles, from base of neck to pelvic area; transition from ventral scales to tubercles ventrolaterally; no ventrolateral skin fold on trunk. Head dorsally and laterally with scales on snout and lips, elsewhere small tubercles. Rostral scale large, rectangular with middorsal cleft; nares bordered by rostral, first supralabial, and 3 nasal scales, supranasal largest. Supralabials 7–12, infralabials 6–10. Broad triangular mental scale ventrally, bordered posteriorly by 2 large anterior chin scales, usually touching one another midventrally; posterior chin scales about half size of anterior ones and rarely touching medially.

Limbs scaled above and below, except for tubercles on posterior surface of thigh. Subdigital lamellae on pad: 6–9 on 4th finger, distal lamella undivided, subsequent 3–7 divided; 7–11 on 4th toe, distal lamella undivided, subsequent 3–7 divided. Bilateral series of 18–27 (total) precloacal-femoral pores in males, left and right sides separated at midpelvic by 1–4 nonpore-bearing scales. Tail midventrally with rectangular, slightly overlapping, smooth-surfaced plates from vent to at least mid-length; large smooth scales ventrolaterally quickly grading into tubercles. Tail distinctly segmented, each segment 8–10 scales long; pair of small erect scales ventrolaterally at posterior edge of each segment.

Hemidactylus geckos can lighten or darken their skin tones. Adults in dark phase, dorsal ground color from head to base of tail medium brown to tan with diffuse, small dark-brown smudges dorsally and dorsolaterally and occasionally with faint white spots to nearly uniform; laterally often series of white spots highlighted by dark-brown smudge in front of each spot. Some individuals with dark-brown postorbital stripe from eye, above ear-opening, to axilla. Dorsal and lateral pattern of white spots bordered by dark marks sharply defined in some population, e.g., Shwe-Settaw. In light phase, dorsum nearly uniform beige or with very faded markings on light background. Ventrally immaculate cream to light yellow from chin through belly; pelvic area and underside of tail light orangish beige.

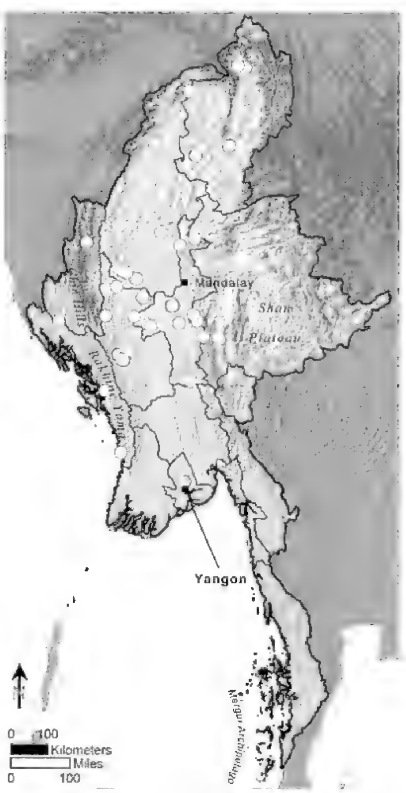

FIGURE 1. Distribution of *Hemidactylus bowringii* in Myanmar based on voucher specimens of the CAS/NWCD/SI Myanmar Herpetological Survey.

Distribution.— Bowring's gecko occurs broadly in Burma (Fig. 1) from the Shan Plateau and adjacent China (Yunnan [CAS specimens] and Sichuan [Zhao 2003]) southward to the Myanmar coast from the western Rakhine to southern Tanintharyi. To the west, its distribution includes northern India — Godavari Valley, Sikkim, Darjeeling — and Bangladesh (Smith 1935), North [=West] Bengal (Tikader and Sharma 1992), and the terai of Nepal (Kästle 2002). This gecko has been reported only thrice from Indochina: three juveniles from Laos (Bourett 1939), one individual from Saigon, Vietnam (Bobrov 1992), and apparently one or a few from northern Vietnam (Darevsky et al. 1984). *H. bowringii* does occur abundantly in some localities in southern China from Hainan westward to Taiwan (Zhao and Adler 1993) and the Ryukyu Islands (Ota 1989).

Because of this gecko's near absence in Indochina, we question the naturalness of its Oriental distribution. Is it an invasive or does the disjunct distribution denote the presence of eastern and western species? Resolving this matter is beyond the scope of this study; however for the moment, we favor the invasive-species explanation. Published evidence (e.g., Karsten et al. 1986; Ota 1989; Lazell 2002) notes its occurrence predominantly or exclusively as a human commensal. Only Lazell (2002) reported it as occurring abundantly in woodlands (disturbed); however, he stated (*in litt*, 9&10 Aug. 2006) that it did not occur in woodlands when *Hemiphyllodactylus chapaensis* was present, and furthermore, *H. bowringii* was abundant and widespread in and around human edifices.

Natural history.— Burmese *Hemidactylus bowringii* is a forest-floor resident. During the day, it occurs beneath leaf litter, logs, and bark. At night, it forages on and beneath the leaf litter. Gravid females from central Myanmar samples were taken in May, July, August, and October.

Hemidactylus brookii (Gray) Asian spiny gecko

Hemidactylus Brookii Gray 1845:153. Type locality, "Borneo." "Australia."; restricted to "Borneo" by Smith (1935:89).

Gecko Tytleri Tytler 1865:547. Type locality, "Moulmein" [= Mawlamyaing, Mon State, Myanmar].

Hemidactylus kushmorensis Murray 1884:109. Type locality, "Bhaner, Upper Sind frontier" [presumably = Bhanar, Sindh, Pakistan].

Hemidactylus Gleadowi Murray 1884:360, Type locality, "Rantha forest in Sind, (Jerruck division)" [= Jerruck region, Pakistan].

Hemidactylus gleadovii Boulenger 1885:129. Amended spelling.

Hemidactylus Murrayi Gleadow 1887:49. Type locality, "Pimpri and Garvi, in the "Dangs", [Gujarat State, India].

Hemidactylus Tenkatei Lidth de Jeude 1895:121. Type locality, "Rotti" [= Pulau Roti (Lesser Sundas), Indonesia].

Hemidactylus subtriedroides Annandale 1905:29. Type locality, "Tsagain, Upper Burma" [= Sagaing, Sagaing Divis., Myanmar].

Hemidactylus brookii parvimaculatus Deraniygala 1953:45. Type locality, "Colombo" [Sri Lanka].

Description.— Adults 45–65 mm SVL; adults sexually dimorphic: females average 53.7±6.28 mm SVL (45.06–61.7 mm); male average 59.6±4.31 mm SVL (50.2–65.0 mm). Moderately robust, slightly flattened lizards. Proportions (female – mean, min.-max.; male – same): SnForel/SVL 38, 35–41%; 37, 33–40%; TrunkL/SVL 41, 36–48%; 42, 39–46%; ForeaL/SVL 12, 11–14%; 12, 10–13%; CrusL/SVL 14, 12–15%; 13, 12–14%. Tail length (unregenerated) slightly longer than SVL and equal in females and males. Tail broader than high (oblong in cross-section), distinctly spiny, and tapering gradually to thin tip.

Head moderately large and broad, distinct from neck, flattened and conical to obovate in dorsal outline. HeadL/SVL 25, 22–27%; 26, 24–29%; JawW/HeadL 64, 57–72%; 62, 51–69%; SnEye/HeadL 40, 35–43%; 40, 35–45%; SnW/HeadL 7, 4–9%; 6, 4–9%. All digits of fore- and hindfeet

with digital pads. Digital pads obovate with distal end slightly wider than proximal base; slender terminal portion (ultimate and penultimate phalanges) of digit arising from within and free of digital pad of all digits. Claws on all digits; slight or no webbing at base of digits.

Head, body, and tail scalation of small, equal-sized, juxtaposed tubercles dorsally and laterally between multiple (14–16) longitudinal rows of enlarged, slightly keeled, conical tubercles; tubercles of parasagittal 2–3 rows slightly smaller and flattened; ventrally, slightly overlapping scales, > 5× dorsal tubercles, from base of neck to pelvic area; transition from ventral scales to tubercles ventrolaterally; no ventrolateral skin fold on trunk. Head dorsally and laterally with scales on snout and lips, elsewhere small tubercles. Rostral scale large, rectangular with middorsal cleft; nares bordered by rostral, first supralabial, and 3 nasal scales, supranasal largest. Supralabials 8–11, infralabials 8–10. Broad triangular mental scale ventrally, bordered posteriorly by 2 large anterior chin scales, broadly touching one another medially; posterior chin scales about two-thirds size of anterior ones and not in contact medially.

Limbs scaled above and below, some large tubercles on anterior and dorsal surface of forearm, more numerous enlarged tubercles on dorsal surface of thigh and crus. Subdigital lamellae on pad: 6–8 on 4th finger, distal lamella undivided, subsequent 5–7 divided; 7–8 on 4th toe, distal lamella undivided, subsequent 5–7 divided. Bilateral series of 11–16 (total) precloacal-femoral pores in males, left and right sides separated at midpelvic by 4–7 nonpore scales. Tail midventrally with rectangular, slightly overlapping, smooth-surfaced plates from vent to at least mid-length; large smooth scales ventrolaterally quickly grading into tubercles. Tail distinctly segmented, each segment 8–10 dorsal scales long; pair of small erect scales ventrolaterally at posterior edge of each segment; dorsally tail distinctly segmented, with middle of each segment bearing roseate of 6 large, keeled conical tubercles.

Adults in dark phase, two-toned brown from head to base of tail, top of head and middorsum onto tail lighter brown than dorsolaterally and sides; sides medium dark-brown to tan; shape and width of lighter middorsal area narrow to broad with broadly scalloped edge; typically in smaller adults and juveniles small dark spots/dashes scattered in both light and dark area; in some individuals, laterally enlarged tubercles lighter than surrounding granular tubercles creating a spotting effect. Many individuals with orbital stripe from snout through eye to ear; broad whitish stripe on snout border above and below by dark border, beyond eye only white stripe and ventral dark border. Ventrally immaculate white to cream from chin to underside of tail. In light phase, two toned dorsum faded but still evident as is faded orbital stripe behind eye. Ventrally immaculate white to cream to light yellow from chin through belly; pelvic area and underside of tail light orangish beige.

Distribution.— Asian *Hemidactylus brookii* occurs widely, but not abundantly, in low elevation areas of north-central Myanmar southward to southern Thaninthary (Fig. 2). Kästle (2002) recognized the taxon *H. brookii subtreidroides* and depicted the latter's occurrence in northern Myanmar and adjacent Arunachal Pradesh. Our survey of

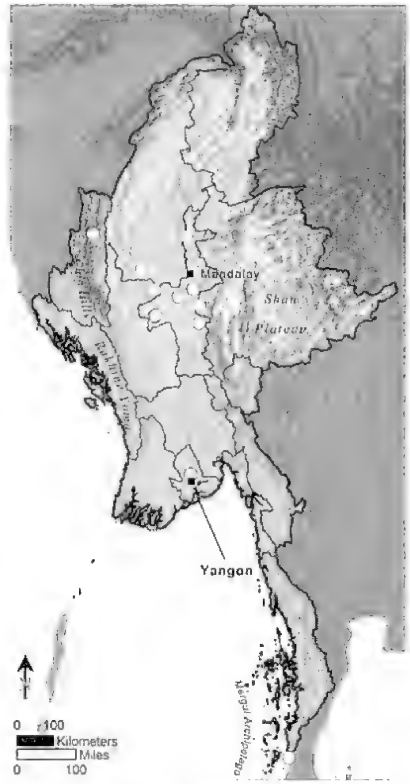

Figure 2. Distribution of *Hemidactylus brookii* in Myanmar based on voucher specimens of the CAS/NWCD/SI Myanmar Herpetological Survey.

sites in northern Sagaing Division has not found *H. brookii* in the northernmost reaches of Myanmar.

The usual description of a nearly pan-tropical distribution for *H. brookii* is applicable only to the paraphyletic concept of this "species." C&A-06's Asian *brookii* still has a broad distribution, but one that naturally lies entirely east of the Indus R. valley. It is a common house gecko in peninsular India and Sri Lanka according to Smith (1935) and others (Sri Lanka, Deraniyagala 1953; India, Daniel 1983). Tikader and Sharma (1992) mapped its occurrence thoughout India. Das (2002), however, reported only a northern India occurrence, and Khan (2002) listed it as a common gecko of the plains of Pakistan and absent from the northern mountains. Kästle (2002) showed a broad terai occurrence and a few records from mid-montane elevations in Nepal. Bauer and Günther (1992) reported a single specimen from the Bhutan-Indian border. Pawar and Birand (2001) found it as human commensal in only two (Nameri National Park, western Arunachal Pradesh, and Balphakaram NP, central Meghalaya) of eight nature reserves surveyed in Northeast India.

As for *H. bowringii*, *H. brookii* is largely absent from Indochina and is excluded from recent reptile field guides (e.g., Cox et al. 1998, Manthey and Grossman 1997) to this area. De Rooij (1915) reports *H. brookii* from Singapore, Sarawak and several Lesser Sunda islands. More recent surveys (Dunn 1927; Darevsky 1964; Auffenberg 1980; Lian 1993) report *H. frenatus*, *H. garnotii*, and/or *H. platyurus* from the latter areas but not *H. brookii*. Denzer and Manthey (1991) noted that the Singapore record was doubtful. Das and Sukumaran (2006) recently documented a single breeding population of *H. brookii* in Borneo.

Southern and eastern China records are limited to Hong Kong and Macau (Karsten et al. 1986) and Zhejiang (Zhao and Adler 1993). Karsten and co-authors stated that it is an introduced species. The Zhejiang record requires investigation, but owing to its presence near Shanghai, it seems likely a record of an introduced population. A similar explanation of introduction is proposed also for the Philippine populations of *H. brookii*; even though it occurs broadly in the Philippines. Brown and Alcala (1978:30) stated: "limited or nearly so to habitats associated with man."

NATURAL HISTORY.— *Hemidactylus brookii* is largely a commensal species in Myanmar, occurring on assorted constructs or on vegetation in the immediate vicinity of manmade structures. Gravid females occur in central Myanmar samples from February and March.

Hemidactylus frenatus Duméril and Bibron — Indo-Pacific house gecko

Hemidactylus javanicus Fitzinger 1826:46. Nomen nudum.

Hemi-dactylus frenatus Kuhl and Van Hasselt in Schlegel 1827:290. Nomen nudum.

Hemidactylus frenatus Duméril and Bibron 1836:366. Type locality, "l'Afrique australe, et . . . tout l'archipel des grandes Indes"; restricted to "Java" by Loveridge (1947:127).

Hemidactylus Bojeri Fitzinger 1843:106. Type locality, "Africa. Madagascar. Mauritus."

Hemidactylus(Pnoëpus) javanicus (Cuv.) Fitzinger 1843:106. Type locality, "Asia. India. Bengala. Ceylon. Java. Timor. Amboina. Ins. Mariannae."; restricted to "Java" by Loveridge (1947:127).

Hemidactylus vittatus Gray 1845:155. Type locality, "Borneo."

Hemidactylus punctatus Jerdon 1853:467. Type locality, "Tellicherry" [= Thalassery, Kerala State, India].

Hemidactylus inornatus Hallowell 1861:469. Type locality, "Loo-Choo" [= Ryukyu Ids.].

Hemidactylus pumilus Hallowell 1861:502. Type locality, "Hong Kong."

Gecko chaus Tytler 1865:547. Type locality, "Moulmein and Rangoon"; restricted to "Rangoon, Burma" by Loveridge (1947:128).

Gecko caracal Tytler 1865:547. Type locality, "Rangoon" [= Yangon, Yangon Divis., Myanmar].

Hemidactylus longiceps Cope 1869:320. Type locality, "Manilla" [= Manila, Luzon Isl., Philippines].

Hemidactylus hexaspis Cope 1869:320. Type locality, "Madagascar."

Peripia papuensis Macleay 1878b:97. Type locality, "Katow" [= Katau, Western Dist., Papua New Guinea].

Hemidactylus tristis Sauvage 1879:49. Type locality, "le nord de la Nouvelle-Guinée."
Hemidactylus nigriventris Lidth de Jeude 1905:188. Type locality, "Sintang [Kalimantan Barat, Indonesia]".
Hemidactylus fragilis Calabresi 1915:236. Type locality, "Bur Meldac" [Somalia].
Hemidactylus vandermeer-mohri Brongersma 1928:1. Type locality, "Pulu Berhala" [= Palau Berhala – there are two].
Hemidactylus okinawensis Okada 1936:271. Type locality, "Okinawa-jima" [Ryukyu Ids.].
Hemidactylus auritus Poeppig in Obst 1977:182. Nomen nudum.

Description.— Adults 42–59 mm SVL; adult SVL sexually dimorphic: females average 45.7±1.98 mm SVL (42.5–49.1 mm); male average 51.1±3.12 mm SVL (47.8–58.6 mm). Moderately built, somewhat flattened lizards. Proportions (female – mean, min.-max.; male – same): SnForel/SVL 36, 33–39%; 38, 35–40%; TrunkL/SVL 46, 39–53%; 43, 40–48%; ForeaL/SVL 12, 10–13%; 12, 10–13%; CrusL/SVL 13, 12–15%; 13, 12–14%. Tail length (unregenerated) slightly longer than SVL and proportionally equal in females and males. Tail round to oblong (broader than high) in cross-section, and tapering gradually to thin tip.

Head moderately large, distinct from neck, flattened and elongate conical (blunt triangular) in dorsal outline, yielding a pointed-snout appearance. HeadL/SVL 25, 24–28%; 25, 25–26%; JawW/HeadL 65, 61–67%; 67, 61–72%; SnEye/HeadL 43, 41–45%; 44, 41–47%; SnW/HeadL12, 12–16%; 13, 12–14%. All digits of fore- and hindfeet with digital pads. Digital pads oblong in shape with distal end only slightly wider than proximal end; slender terminal portion (ultimate and penultimate phalanges) of digit arising from within and free of digital pad of all digits. Claws on all digits; slight or no webbing at base of digits.

Head, body, and tail scalation of small, equal-sized, juxtaposed tubercles dorsally and laterally with several longitudinal rows (about 6) of widely spaced enlarged tubercles (flatten cones, usually unkeeled); ventrally, slightly overlapping scales, 4–5× dorsal tubercles, from base of neck to pelvic area; transition from ventral scales to tubercles ventrolaterally; no ventrolateral skin fold on trunk. Head dorsally and laterally with scales on snout and lips, elsewhere small tubercles. Rostral scale large, rectangular with middorsal groove; nares bordered by rostral, first supralabial, and 3 nasal scales, supranasal largest. Supralabials 9–12, infralabials 7–10. Triangular mental scale ventrally, bordered posteriorly by 2 large anterior chin scales, in contact with one another midventrally; posterior chin scales from subequal to about half size of anterior ones and not touching medially.

Limbs scaled above and below, except for tubercles on posterior surface of fore- and hindlimbs. Subdigital lamellae on pad: 7–9 on 4th finger, distal lamella undivided, subsequent 5–7 divided; 8–11 on 4th toe, distal lamella undivided, subsequent 5–8 divided. Bilateral series of 23–34 (total, usually ≥29) precloacal-femoral pores in males, left and right sides separated at midpelvic by 0–2 nonpore scales. Tail midventrally with rectangular, slightly overlapping, smooth-surfaced plates from 8–12 scale rows behind vent to at least mid-length; 2–3 rows of large smooth scales ventrolaterally grading into tubercles. Tail distinctly segmented, each segment 10–12 scales long; each segment with 6 (usually) enlarged flattened cone-shaped scales projecting above surface; projecting scales inset about 2 small tubercle rows from rear edge of segment and ventrolateral pair largest in each spiral.

Adults in dark phase, dorsal ground color from head to base of tail dusky brown dorsally, lighter brown stripe from snout through eye above ear to trunk fading thereafter, and dark brown stripe from snout on upper lip through shoulder and distinct to hindlimbs. Preceding bold pattern uncommonly seen; often only marking is faded lateral stripe from snout to shoulder. In light phase, dorsum uniform whitish gray without markings. Ventrally whitish to light beige in all color phases from chin onto underside of tail.

Distribution.— *Hemidactylus frenatus* occurs broadly throughout Myanmar (Fig. 3) from north-central Sagaing Division and central Kachin State southward to the coast of Tanintharyi, Mon, Yangon, Ayeyarawady, and Rakhine. It is a common house gecko from India eastward through tropical Asia and Indoaustralia to the central Pacific. Sharma (2002: map 29) excluded *H. frenatus* from India north of 24°N.

Natural history.— Our surveys reveal that *Hemidactylus frenatus* is always associated with man-made structures. Gravid females occur in central Myanmar samples from May and July.

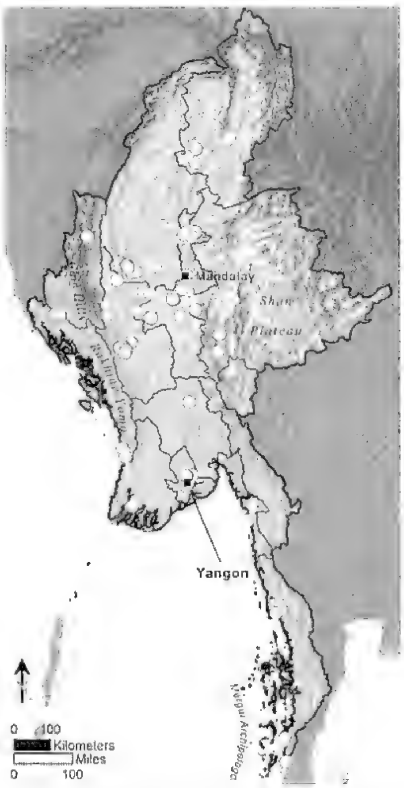

Figure 3. Distribution of *Hemidactylus frenatus* in Myanmar based on voucher specimens of the CAS/NWCD/SI Myanmar Herpetological Survey.

Hemidactylus garnotii Duméril and Bibron
Fox gecko

Hemidactylus peruvianus Wiegmann 1835:240. Type locality, "Peru, bei Tacna"; probably in error, see taxonomic comments in Bauer (1994).

Hemidactylus Garnotii Duméril and Bibron 1836:368. Type locality, "l'île de Taïti" [= Tahiti, French Polynesia].

Doryura vulpecula Girard 1857:197. Type locality, "Sandwich Islands" [= Hawaiian Islands].

Hemidactylus Ludekingii Bleeker 1859a:27. Type locality, "Agam, Padangsche bovenlande" [= Agam, Sumatra].

D.[*oryura*] *gaudama* Theobald 1868:30. Type locality, "Tonghu (valle Sittangensi)." [= Taungoo (Sittaung R. valley), Bago Divis., Myanmar].

H.[*emidactylus*] *Mortoni* Theobald 1868:32. Type locality, "Teikgyie" [= Taikkyi, Yangon Divis., Myanmar].

Hemidactylus (*Doryura*) *mandellianus* Stoliczka 1872:101. Type locality, "Pankabari [Sikkim, India], just above the Sikkim Terai, and . . . the Rungnu and Tístá valleys".

Hemidactylus blanfordii Boulenger 1885:141. Type locality, "Himalayas." "Darjeeling [West Bengal State, India]."

Description.— Adults 49–66 mm SVL, average 56.5±5.13 mm; female only species. Moderately built, somewhat flattened lizards. Proportions (mean, min.-max.): SnForel/SVL 39, 37–43%; TrunkL/SVL 43, 39–46%; ForeaL/SVL 11, 10–13%; CrusL/SVL 13, 11–14%. Tail length (unregenerated) distinctly longer than SVL, about 1.2×. Tail flattened, broader than high (oblong in cross-section), and tapering gradually to thin tip.

Head moderately large and broad, distinct from neck, flattened and elongate triangular and snout truncate in dorsal outline. HeadL/SVL 25, 24–26%; JawW/HeadL 63, 60–72%; SnEye/HeadL 46, 40–47%; SnW/HeadL 12, 10–14%. All digits of fore- and hindfeet with digital pads. Digital pads oblong in shape with distal end only slightly wider than proximal end; slender terminal portion (ultimate and penultimate phalanges) of digit arising from within and free of digital pad of all digits. Claws on all digits; slight or no webbing at base of digits.

Head, body, and tail scalation of small, equal-sized, juxtaposed tubercles dorsally and laterally; slightly overlapping scales, >5× dorsal tubercles, ventrally from base of neck to pelvic area; transition from ventral scales to tubercles ventrolaterally; no ventrolateral skin fold on trunk. Head dorsally and laterally with scales on snout and lips, elsewhere small tubercles. Rostral scale large, rectangular with middorsal cleft; nares bordered by rostral, first supralabial, and 3 nasal scales,

supranasal largest. Supralabials 8–13, infralabials 7–10. Triangular mental scale ventrally, bordered posteriorly by 2 moderately large anterior chin scales, in contact midventrally; posterior chin scales two-thirds or less size of anterior ones, rarely touching medially, and regularly separated from infralabials by row of smaller gular scales.

Limbs with moderate-size tubercles above and smooth scale below. Subdigital lamellae on pad extending to base of digit and slightly on to palm/sole: 8–13 on 4th finger, distalmost lamella undivided, subsequent 5–8 divided; 10–15 on 4th toe, distalmost lamella undivided, subsequent 5–8 divided. No precloacal-femoral pores. Tail midventrally with rectangular, slightly overlapping, smooth-surfaced plates from vent to at least mid-length; large smooth scales ventrolaterally quickly reducing in size to small elongate conical scales on ventrolateral edges. Tail distinctly segmented, each segment 8–10 scales long; ventrolaterally sawblade-like with four conical "spine" scales in each segment, posteriormost one at edge of each segment double the size of preceding three.

Adults in dark phase, dorsal ground color from head to base of tail grayish or yellowish tan to medium brown with five longitudinal rows (middorsal, dorsolateral, and lateral) of whitish spots from nape/neck to rump; on lighter background spots in diffuse brown longitudinal stripes. Only middorsal spots on tail, 2–3× larger than on trunk and often dark edged anteriorly. Most individuals, light or dark phase, with dark-brown postorbital stripe from eye to above ear-opening; this stripe occasionally in front of eye to snout and/or continuous with white spot-bearing lateral stripe. In light phase, dorsum nearly uniform beige or with faded markings on light background. Ventrally immaculate cream to light yellow from chin onto underside of tail.

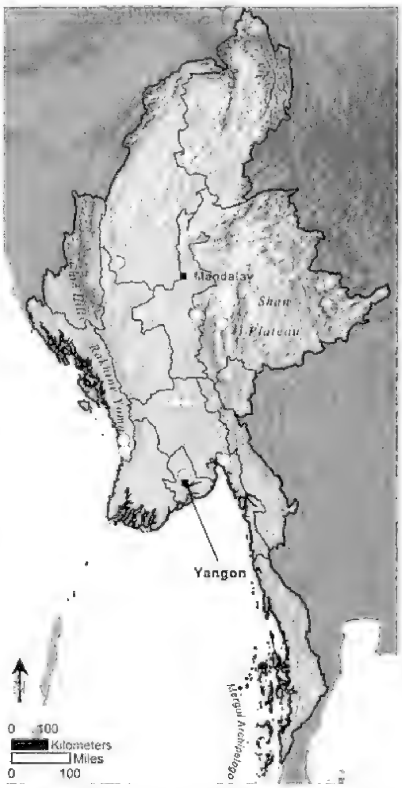

FIGURE 4. Distribution of *Hemidactylus garnotii* in Myanmar based on voucher specimens of the CAS/NWCD/SI Myanmar Herpetological Survey

DISTRIBUTION.— *Hemidactylus garnotii* occurs widely, although nowhere abundantly, throughout Myanmar (Fig. 4), largely a low elevation distribution from southern Sagaing Division and central Kachin State southward to the Martaban coast from Rakhine to Mon States.

Its extralimital distribution is broad although spotty with populations established in the Bahamas and southern Florida (USA), throughout the Pacific, and Islands Asia, East Asia westward to Pakistan, and southward to the Seychelles. Tikader and Sharma (1992: map 8) showed its presence in India restricted to Sikkim eastward into central Assam. The recognition of two karyotypically different species (*H. vietnamensis*, Vietnam; *H. stejnegeri*, Taiwan, Ryukyu Islands and likely all of the Philippine Islands [Ota and Hikida, 1989]) suggests a more careful assessment of individual Asian populations before a broad-brush assignment to *H. garnotii*.

NATURAL HISTORY.— The few *H. garnotii* captured were either on buildings or immediately adjacent to human constructs. Gravid females occur in central Myanmar samples taken only in February.

***Hemidactylus karenorum* (Theobald)** Burmese spotted gecko

D.[*oryura*] *Karenorum* Theobald 1868:30. Type locality, "Karen-choung, prope Toungoo, valle Sittangensi" [= Karenchaung, above Taungoo, Sittang R. valley, Bago Divis., Myanmar].

Description.— Adults 38–56 mm SVL; adult SVL not sexually dimorphic: females average 50.2±3.56 mm SVL (45.7–56.1 mm); male average 47.2±5.68 mm SVL (38.3–55.8 mm). Moderately built, somewhat flattened lizards. Proportions (female – mean, min.-max.; male – same): SnForel/SVL 38, 36–42%; 38, 36–41%; TrunkL/SVL 41, 38–43%; 42, 39–48%; ForeaL/SVL 12, 11–13%; 12, 11–14%; CrusL/SVL 13, 12–14%; 14, 13–15%. Tail length (unregenerated) approximately equal to SVL in both females and males. Tail flattened, broader than high (semicircular to spindle-shape in cross-section), and tapering gradually to thin tip.

Head moderately large and broad, distinct from neck, flattened and conical to obovate in dorsal outline. HeadL/SVL 25, 24–26%; 26, 25–28%; JawW/HeadL 65, 62–70%; 63, 58–71%; SnEye/HeadL 43, 42–45%; 43, 42–46%; SnW/HeadL 13, 12–15%; 13, 11–15%. All digits of fore- and hindfeet with digital pads. Digital pads oblong to obovate in shape with distal end usually wider than proximal end; slender terminal portion (ultimate and penultimate phalanges) of digit arising from within and free of digital pad of all digits. Claws on all digits; slight or no webbing at base of digits.

Dorsal and lateral scalation of head and body of small, equal-sized, juxtaposed tubercles interspersed with numerous smooth-surfaced cone-shaped tubercles (area of each about 3 smaller background tubercles); usually cone-shaped tubercles densely packed on body and without a longitudinal arrangement into rows; dorsally fewer enlarged tubercles on tail and more longitudinally; ventral scales slightly overlapping, about 5× smaller dorsal tubercles; transition from ventral scales to tubercles ventrolaterally; no ventrolateral skin fold on trunk. Head dorsally and laterally with scales on snout and lips, elsewhere small tubercles. Rostral scale large, rectangular with long median cleft, about two-thirds height of rostral; nares bordered by rostral, first supralabial, and 3 nasal scales, supranasal largest. Supralabials 10–12, infralabials 7–11. Broad triangular mental scale ventrally, bordered posteriorly by 2 large anterior chin scales, in contact medially; posterior chin scales equal size of anterior ones and not touching medially.

Limbs uniformly scaled above and below, except for small tubercles on posterior surface of thigh. Subdigital lamellae on pad: 7–9 on 4th finger, distal lamella undivided, subsequent 4–7 divided; 8–10 on 4th toe, distal lamella undivided, subsequent 5–7 divided. Bilateral series of 26–38 (total and most >34) precloacal-femoral pores in males, left and right sides separated at midpelvic by 1–3 nonpore scales. Tail midventrally with rectangular, slightly overlapping, smooth-surfaced plates from vent to at least mid-length; large smooth scales ventrolaterally quickly grading into lateral fringe scales. Tail distinctly segmented, each segment 8–10 scales long; dorsal scale small, smooth and slightly overlapping; lateral edge of tail fringed with modestly enlarged triangular scales, 3–4 per segment, usually posterior-most one of each segment larger than other, yielding a ragged saw-like fringe.

Adults in dark phase, dorsal ground color from snout onto tail medium brown to grayish khaki; head uniform to diffusely mottled in light and medium brown; dark irregular rectangular spots on dorsum from nape to base of tail; usual spot pattern of dorsum, row of about six spots on midline from nape onto tail, dorsolateral row of spots, and lateral row on trunk often fused into nearly continuous stripe. Most dark phase individuals with dark-brown postorbital stripe from snout through eye and ear to axilla continuous with lateral trunk stripe. In light phase, dorsum nearly uniform beige or with faded markings on light background. Ventrally immaculate cream to light yellow from chin onto tail.

Distribution.— Our survey data suggest that *Hemidactylus karenorum* may be a Burmese endemic (Fig. 5), although it might reach the eastern mountains in Bangladash. Our specimen-vouchers limit this species' occurrence to the central and north-central portion of the Ayeyarwady River valley, even absent from the northern portion of the Sittaung River drainage. We have not yet had the opportunity to examine the specimen reported (Smith 1935) from Assam, but the absence of this species from our survey sites in the northern half of the Chindwin River basin suggests a misidentification of the Assam specimen. Tikader and Sharma (1992) listing of *H. karenorum* from Assam appears to be a repeat of Smith's (1935) earlier report. As yet, we are unable to locate the specimen ["Cachar in Assam"] reported by Smith. The BMNH has only four *karenorum* specimens, and they represent two Burmese localities.

Natural history.— *Hemidactylus karenorum* is a forest gecko, commonly found in leaf litter along streams or the base of trees.

Gravid females were found in central Myanmar samples taken in February and March.

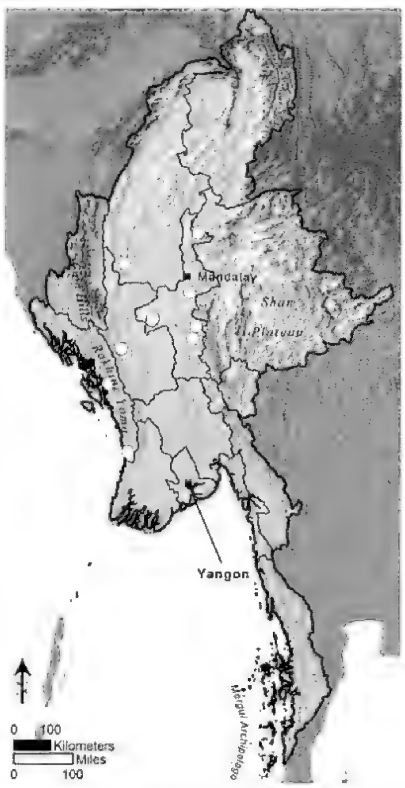

FIGURE 5. Distribution of *Hemidactylus karenorum* in Myanmar based on voucher specimens of the CAS/NWCD/SI Myanmar Herpetological Survey.

Hemidactylus platyurus (Schneider)
Asian flat-tailed gecko

Stellio platyurus Schneider 1792:30[62]. Type locality, none given.
Lacerta Schneideriana Shaw 1802:278. Subsitute name for *Stellio platyurus* Schneider.
G[*ecko*] *marginata* Cuvier 1829:55. Type locality, "Bengale." [original description not seen]
Nycteridium schneideri Günther 1864:111. Subsitute name for *Stellio platyurus* Schneider.
Nycteridium Himalayanum Anderson 1871:15. Type locality, "Darjeeling; 3000 feet" [West Bengal State, India].
Hemidactylus nepalensis Annandale 1907:151. Type locality, "Kathmandu, Nepal: altitude 4,500 feet."

Description.— Adults 47–58 mm SVL; adult SVL and not sexually dimorphic in any traits: females average 53.2±2.94 mm SVL (47.5–50.7 mm); male average 51.8±3.63 mm SVL (49.2–58.1 mm). Moderately built, somewhat flattened lizards. Proportions (female – mean, min.-max.; male – same): SnForel/SVL 36, 34–38%; 36, 33–38%; TrunkL/SVL 46, 40–51%; 45 44–46%; ForeaL/SVL 11, 11–12%; 12, 11–12%; CrusL/SVL 12, 11–14%; 13, 11–15%. Tail length (unregenerated) subequal to or slightly longer than to SVL and equal in females and males. Tail strongly flattened, much broader than high, and elongate dagger-like from base to pointed tip, lateral edges serrated with flatten, pointed scales.

Head moderately large and broad, distinct from neck, flattened and broad-triangular to pentagonal in dorsal outline. HeadL/SVL 24, 23–25%; 24, 22–25%; JawW/HeadL 67, 63–74%; 68, 63–73%; SnEye/HeadL 42, 40–46%; 42, 40–47%; SnW/HeadL 15, 14–17%; 14, 14–16%. All digits of fore- and hindfeet with digital pads. Digital pads obovate in shape with distal end slightly wider than proximal end; slender terminal portion (ultimate and penultimate phalanges) of digit arising from within and free of digital pad of all digits. Claws on all digits; modest webbing, about one-third length of digits on fore- and hindfeet.

Head, body, and tail scalation of small, equal-sized, juxtaposed tubercles dorsally and laterally, including the trunk skin-fold; slightly overlapping smooth scales, >5× dorsal tubercles, ventrally from base of neck to pelvic area; transition from ventral scales to tubercles ventrolaterally, 5–6 scale rows from base of skin-fold; distinct ventrolateral skin fold on trunk, posterior edge of thigh and crus, and often on anterior edge of upper arm. Head dorsally and laterally with scales on snout and lips, elsewhere small tubercles. Rostral scale large, rectangular with middorsal cleft; nares bordered by rostral, first supralabial, and 3 equal-sized nasal scales. Supralabials 9–13, infralabials 8–11. Broad triangular mental scale ventrally, bordered posteriorly by 2 large anterior chin scales, usually broadly in contact medially; posterior chin scales half or less the area of anterior ones and broadly separated medially.

Limbs covered above and below with granular scales (about 2× dorsum scales), except for smooth scales on posteroventral surface of thigh. Subdigital lamellae on pad: 7–9 on 4th finger, distal lamella undivided, subsequent 5–7 divided; 6–9 on 4th toe, distal lamella undivided, subsequent 5–7 divided. Bilateral series of 36–40 (total) precloacal-femoral pores in males, left and right sides separated at midpelvic by 1–4 nonpore scales. Tail midventrally with rectangular, slightly overlapping, smooth-surfaced plates from vent to near tip; large smooth scales ventrolaterally quickly grading into tubercles. Tail indistinctly segmented, evident only by enlarged lateral-edge spine at posterior edge of each segment, segments 8–9 scales long; ventrolateral edge with series of spine-like scales, last one largest on each segment.

Adults in dark phase, dorsal ground color from head to base of tail medium brown to dusky tan with scattered small, elongate dark-brown spots dorsally, occasionally dorsolateral spots coalesced into dorsolateral stripe from posterior corner of eye (rarely from tip of snout) to shoulder, laterally broad dark-brown stripe from loreal area to inguen. Some individuals with beige stripe between dark-brown stripes from snout through eye to ear-opening. Dorsum of tail variably banded with dark and light brown, dark bands subequal to twice width of light ones.

In light phase, dorsum nearly uniform beige, rarely with diffused mottling on light background. Ventrally immaculate cream to light yellow from chin onto tail.

COMMENT.— Our survey has collected a few individuals from southern Tanintharyi, two of which are males — a subadult and an adult. Neither of these individuals displays precloacal-femoral pores or the precursor pits. None of the other traits are strikingly different from the central Myanmar *H. platyurus* sample. This observation and those of M. Smith's (1935) suggest the potential of regional differentiation. The inclusion of images of both *H. craspedotus* and *H. platyurus* in the Cox et al. (1998) *H. platyurus* account potentially exaggerates our interpretation of pattern variation in the latter species.

DISTRIBUTION.— Even though *Hemidactylus platyurus* occurs from about 26°N to the southern most tip of Myanmar (~10°N), our survey records (Fig. 6) show a very spotty occurrence and, at least for central and northern Myanmar,

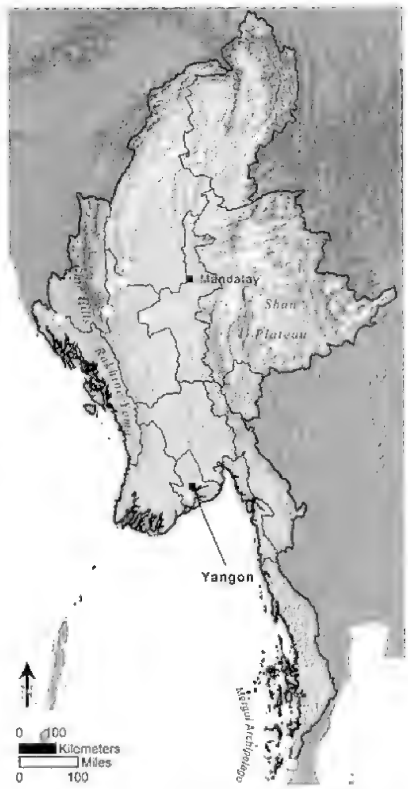

FIGURE 6. Distribution of *Hemidactylus platyurus* in Myanmar based on voucher specimens of the CAS/NWCD/SI Myanmar Herpetological Survey.

no populations in the Ayeyarwady valley or in the foothills and mountains to the east. Tikader and Sharma (1992) also reported a limited distribution (Sikkim, Darjeeling District) in India; furthermore, their statement of its commensal habits suggests a human introduction into the Darjeeling area. Ulber and Ulber (1991) provided a general distribution map of *H. platyurus*, showing a broad distribution from Sri Lanka and eastern India through South Asia to the Philippines and New Guinea. They further noted that this species occurs exclusively in the vicinity of human habitation. Our natural history note below offers a slight contradiction to this exclusivity; however, its high human commensalism likely explains its broad distribution via accidental transport.

NATURAL HISTORY.— Most individuals were captured in or on buildings, otherwise two individuals from a sandstone wall of a stream-cut and one from the forest floor.

Gravid females were found in central Myanmar samples taken in June and July, although other adults from these samples were only in early to mid-vitellogenesis.

TAXONOMIC NOTES ON TROPICAL ASIAN *HEMIDACTYLUS*

The results of Carranza and Arnold (2006; abbrev. C&A-06) encouraged the current investigation of Burmese *Hemidactylus*. The C&A-06 molecular (mtDNA) phylogeny demonstrated that *Hemidactylus* is monophyletic when *Cosymbotus platyurus* is returned to *Hemidactylus* as proposed by Boulenger (1885). Additionally, their analysis revealed five clades, each of which represents a distinct geographic and evolutionary arena. Their tropical Asian clade ((*platyurus* (*bowringii* (*karenorum*, *garnotii*)) (*flavivirdis* (*brookii*, *frenatus*))) (Fig. 7) contains seven of the approximately 20 species know to occur naturally from the Indus River eastward through tropical Asia. We assume for the following discussion that all Asian *Hemidactylus* are members of the C&A-06's tropical Asian clade. We have not attempted a morphological comparison to locate a synapomorphic trait that supports this assumption. Such a comparison would be useful, and critically, a broader DNA sampling of tropical Asian *Hemidactylus* is essential to test the monophyly of this putative Asian clade.

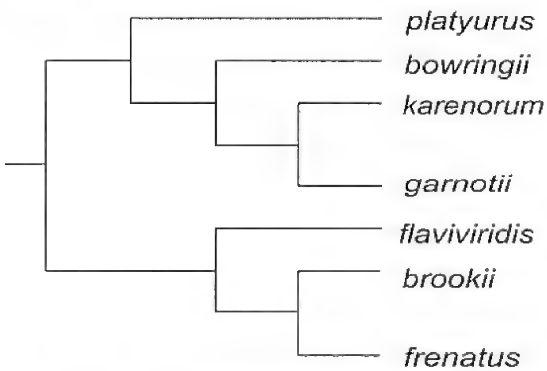

FIGURE 7. Stylized dendrogram displaying the proposed relationships among members of the tropical Asian clade of *Hemidactylus*. The dendrogram derives from the maximum likelihood tree of Carrenza and Arnold (2006: fig. 1).

The monophyly of tropical Asian *Hemidactylus* creates a taxonomic unit that contains about three times as many species (Table 1) as studied by C&A-06. We share C&A-06's unwillingness [implied] to assign formal taxonomic names to this or any of the other identified clades. Formal name assignment of generic or subgeneric names for each of the clades would be easy owing to the surfeit of synonyms for the genus *Hemidactylus*. A partitioning of the genus, however, without a further testing of the monophyly of the five clades is premature and will only obfuscate the affinities of *Hemidactylus* geckos, particularly when less than a quarter of the known species were included in C&A-06's phylogenetic analysis.

Our only exception to a change in generic assignment is reverting to Boulenger's 1885 usage of *Hemidactylus platyurus*. We believe this usage is now necessary in any discussion of Asian *Hemidactylus*. Shifting *platyurus* to *Hemidactylus* restores the combination *H. craspedotus* Mocquard, 1890. This latter taxon became *Mimetozoon craspedotus* when de Rooij (1915) assigned the

TABLE 1. Putative species of the tropical Asian clade of *Hemidactylus*. Species names are arranged chronological. Only those taxa currently recognized as valid by Kluge (2001) and Bauer (1994) are listed. Type localities are in brackets and generalized; species occurring in Burma in bold.

1792	***Stellio platyurus*** Schneider [not stated]
1802	*Gecko triedrus* Daudin [not stated]
1835[1]	*Hemidactylus flavivirdis* Rüppell [Massaua Isl. Eritrea]
1836	***Hemidactylus frenatus*** Duméril & Bibron[2] [Java]
1836	***Hemidactylus garnotii*** Duméril & Bibron [Tahiti]
1836	*Hemidactylus leschenaultii* Duméril & Bibron [Sri Lanka]
1836	*Hemidactylus maculatus* Duméril & Bibron [Bombay Pres., India]
1842	*Hemidactylus depressus* Gray [Madagascar]
1845	***Doryura bowringii*** Gray [Hong Kong]
1845	***Hemidactylus brookii*** Gray [Borneo]
1854	*Hemidactylus subtriedus*[3] Jerdon [Madras Pres., India]
1861	*Hemidactylus marmoratus*[4] Hallowell [Ryukyu Ids.]
1868	***Doryura karenorum*** Theobald [Myanmar]
1870	*Hemidactylus reticulatus* Beddome [eastern Karnataka, India]
1870	*Hemidactylus gracilis* Blanford [Central Prov., India]
1871	*Hemidactylus giganteus* Stoliczka [Godavari Valley, India]
1875	*Gecko anamallensis* Günther [Western Ghats, India]
1890	*Hemidactylus craspedotus* Mocquard [Borneo]
1906	*Tetratolepis scabriceps* Annandale [southern Tamil Nadu, India]
1935	*Hemidactylus prashadi* M.A. Smith [Bombay Pres., India]
1981	*Hemidactylus porbandarensis* Sharma [Gujarat, India]
1984	*Hemidactylus mahendrai* Shukla [Uttar Pradesh, India]
1984	*Hemidactylus vietnamensis* Darevsky & Kupriyanova [northern Vietnam]
1989	*Hemidactylus stejnegeri* Ota & Hikida [Taiwan]

[1] Kluge gives dates as 1840, presumably because the latter sections of this publication appeared over several years.

[2] Kluge credits authorship to Schlegel 1836.

[3] Smith (1935) considered *H. subtriedus* questionably distinct from *H. triedrus*. Its absence from Das' (2002) pocket guide indicates a similar opinion.

[4] Kluge recognized *H. marmoratus* as a valid taxon, yet Ota (1989) does not include it as a member of the Ryukyu gecko fauna. Smith (1935) synonymized it with *H. leschenaultii*.

type species *Mimetozoon floweri* Boulenger, 1897 to the synonymy *H. craspedotus* and retained *Mimetozoon* for this gecko with large bilateral body folds and well-webbed digits. She retained the combination *Hemidactylus platyurus*. Subsequently, Smith (1935) synonymized *Mimetozoon* Boulenger, *Nycteridium* Günther, 1864, and *Cosymbotus* Fitzinger, 1843 with *Platyurus* Oken, 1836 (see Taylor, 1963, for additional history). Thereafter, these two species regularly shifted between the latter two genera and only with Wermuth's 1965 checklist attained stability in assignment to *Cosymbotus*.

Nowhere in this history of generic reassignments did anyone examine the affinities of *craspedotus* and *platyurus* to one another or to other *Hemidactylus* species. The body folds and digital webbing kept these two taxa closely linked for the last 70 years. C&A-2006's study does not address the relationship of these two species, but it does eliminate the implied relationships of shared generic assignment outside of the genus *Hemidactylus*. It is such implied relationship that argues against the use of formal group names for the various *Hemidactylus* geographic clades.

As previously noted, the C&A-2006 phylogram (Fig. 7) addresses the relationships of only a

third of the members of the putative tropical Asian clade. The phylogram indicates two lineages or clades (*bowringii-garnotii-karenorum-platyurus* and *brookii-flaviviridis-frenatus*). [Hereafter, we use complex for the *bowringii* and *brookii* clades as a phylogenetically neutral label.] Two questions immediately derive from this proposed relationship: 1) Do these two complexes encompass all the tropical Asian *Hemidactylus* or, as additional Asian taxon are examined, will new clades emerge and/or change the composition of current ones? 2) Do the members of each of these clades display a set of morphological traits that permit the visual differentiation of the complexes and assignment of molecularly untested Asian species to one or the other of the complexes? We cannot address the first question as a solution requires a broader molecular sampling of Asian species. This question, however, draws attention to a serious flaw of the C&A-06 study, i.e., inadequate specimen vouchering of their molecular samples. Only about a quarter of the C&A-06 DNA-samples have voucher specimens on which species identification can be re-examined and confirmed. An example of the problems arising from unvouchered samples is the identity of their Thiruvanan-Indian "*Hemidactylus frenatus*." It is likely not a *H. frenatus* as currently conceived throughout the '*frenatus*' broad invasive-distribution. The specimens from recently invaded areas (Colombia and Hawaii) are genetically identical to one another and paired with Burmese specimens (C&A-06: fig. 1; our Fig. 7). The Indian *H. frenatus* is genetically distinct from the Burmese-Invasive lineage, thereby hinting that *Hemidactylus punctatus* Jerdon, 1854 may be a valid taxon, because the C&A-06 sample derived from Thiruvananthapuram, Kerala, about 350 km south of the type locality (Tellicherry) of Jerdon's species. This possibility cannot be examined further without a voucher specimen for the molecular data.

Returning to the second question, a superficial morphological survey of C&A-06's tropical Asian species identified a set of traits (trunk scalation, tail ornamentation, digital lamellae, and precloacal-femoral pores) that generally delimits the two Asian complexes. The *bowringii* complex either lack ornamentation on the tail or the spines are confined to the ventrolateral margin as a single scale-spine or a fringe of unequal sized scale-spines on each side of each caudal segment. Tail ornamentation in the *brookii* complex consists of a circumferential row or rows of scale-spines on each segment. The number of rows, numbers of spines, and relative size of the spines vary between the species, with *H. brookii* having the most spinose tail. Trunk scalation (back and sides) consists of uniformly small juxtaposed (granular) scales in the *bowringii* complex, except for *H. karenorum* with its irregular longitudinal rows of small tubercles. The *brookii* complex members have numerous longitudinal rows of variously developed tubercles on the trunk, except for *H. flaviviridis*, which lacks tubercles. A third to half of the digital lamellae on each digit of *bowringii* complex are divided, in contrast to only the terminal lamellae of the *brookii* complex are undivided. Precloacal-femoral pores occur only in males and are typically continuous across the hindlimb-pelvic junction. Members of the *bowringii* complex regularly possess a total of 26 pores or more, whereas *brookii* members usually have a total of 18 or fewer, except for *H. frenatus* commonly ≥ 24 pores. With more pores on each side, *bowringii* members have fewer (0–3) nonpore scales separating the left and right rows of pore-scales, and *brookii* members ≥ 4 nonpore scales, except for *H. frenatus* (0–1).

These traits allow a hypothetical assignment of the molecularly untested tropical Asian *Hemidactylus* to the two complexes: *bowringii* complex — *anamallensis*, *craspedotus*, *depressus*, *giganteus*, *leschenaultii*, *stejnegeri*, and *vietnamensis*; *brookii* complex — *maculatus*, *prashadii*, *reticulatus*, and *triedrus*. Several taxa are not assigned: 1) *marmoratus* and *subtriedus* are not considered valid taxa (see footnotes of Table 1); 2) *gracilis* has 10–12 longitudinal rows of well-developed tubercles on the trunk and a tail oblong in cross-section without ornamentation, sharing a major trait of each complex, but more critically only precloacal pores [a trait shared only with *H. porbandaren-*

sis among tropical Asian *Hemidactylus*, although approached in some *brookii* complex members]; 3) *porbandarensis* [possibly a *brookii* complex member] has 16–17 longitudinal rows of enlarged, keeled tubercles on the trunk dorsum, moderately compressed tail, presumably with transverse rows of six spines at edge of each segment, and a short row of precloacal pores; 4) Annandale's description of *scabriceps* reported dorsal trunk scales imbricate and equal in size to the belly scales [a trait not known elsewhere in tropical Asian *Hemidactylus*]. Shukla's description (1984) of *H. mahendrai* is based on a few juvenile and female specimens. Further, the description lacks a statement differentiating *H. mahendrai* from *H. brookii*, although diagnostic traits are provided for other Indian *Hemidactylus* species. Shukla's description match the traits of female Asian *H. brookii*, thus we tentatively suggest that *mahendrai* is a synonym of the latter species. The uncertainty of assignment for the latter two taxa urges their inclusion in the next molecular phylogenetic analysis.

The preceding taxon assignment derived mainly from the states of trunk scalation, tail ornamentation, and precloacal-femoral pore number. *Hemidactylus leschenaultii* has some enlarged dorsal tubercles, but tail ornamentation and precloacal-femoral pores are strongly *bowringii* complex. *Hemidactylus depressus* similarly has numerous rows of dorsal tubercles and otherwise has *bowringii* complex traits. We note that *H. karenorum* also has numerous tubercles, although smaller than the *brookii* complex condition, smooth and rounded, and not arranged in longitudinal rows. Ignoring the high number of pores in *H. depressus*, *bowringii* complex assignments were unequivocal.

Hemidactylus stejnegeri and *H. vietnamensis* are all-female species and without karyotypic data would have remained unrecognized as distinct genetic lineages from *H. garnotii*. *Hemidactylus vietnamensis* was recognized by Darevsky and colleagues (1984) when they obtained karyotypes from northern Vietnam *H. garnotii*. Contrary to Kluge and Eckardt's karyotypic results (3n = 70; Kluge and Eckardt 1969) for Floridian and Hawaiian *H. garnotii*, the karyotype of the Vietnamese "*garnotii*" specimens was 3n = 60. Darevsky et al. (1984: table 2) contrasted seven scalation traits of their Vietnamese specimens (n = 17) with a subset (n = 28) of Kluge and Eckardt's Hawaiian sample (n = 66) and found significant differences in 6 traits. The scalation and karyotypic differences led them to recognize the Vietnamese population as a distinct species. These scalation differences are slight and might result from differences in trait definition and data-collection; however, Ota et al. (1986) examined a set of 7 traits in the Kluge-Eckardt Hawaiian, Darevsky et al. Vietnamese, and 3 Chinese (Yunnan, Hainan, Taiwan) samples. This analysis confirmed the distinctiveness of the Hawaiian and Vietnamese samples from one another. The Hainan and Yunnan samples were not significantly different from one another, but combined they differed modestly from the Hawaiian and Taiwan samples, and strongly differentiated from the Vietnamese one.

Subsequently, Ota and Hikida (1989b) examined the karyotypes of Taiwanese "*garnotii*" and discovered another karyotype (3n = 56) and recognized this population as *H. stejnegeri*. In a series of research articles, Ota and collaborators examined karyotypic evolution and the origin of parthenogenesis in unisexual *Hemidactylus*. Their general conclusion is that there are two parthenogenetic groups: the *H. garnotii-vietnamensis* complex and *H. stejnegeri*. Both groups arose by hybridization, and presently, evidence identifying the parental species is not available. They also discussed the likelihood of karyotypic evolution without concomitant morphological differentiation within a unisexual species. We lack data and expertise to support or negate their hypothesis of relationships and accept their assessment of two clonal lineages. The C&A06 molecular data show genetic uniformity within Burmese *H. garnotii* and between Burmese and Floridian specimens. Moritz et al. (1993) showed a uniformity of *H. garnotii* karyotype number (3n = 63) among Pacific island populations, including Hawaii, and the Florida population. They also noted a low diversity of allozymes and mtDNA among their samples. Combing there results with those of C&A-06

indicates that the Burmese populations is *H. garnotii*. Nevertheless until there is a molecular analysis among the various Asian populations of the parthenogens, we urge caution on assigning the name *garnotii*.

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A Revision of *Symplocos* Jacq. Section *Neosymplocos* Brand (Symplocaceae)

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A taxonomic revision of *Symplocos* Jacq. section *Neosymplocos* Brand is provided to replace the outdated 1901 treatment of Brand. A total of 780 specimens and 17 photographic images from 23 herbaria was examined to evaluate the taxonomic importance of morphological characteristics. Eleven species are recognized (*S. altissima*, *S. angulata*, *S. corymboclados*, *S. falcata*, *S. glandulosomarginata*, *S. glaziovii*, *S. insolita*, *S. microstyla*, *S. nitidiflora*, *S. organensis*, and *S. tenuifolia*), one new name is proposed (*S. insolita*), and several names are lectotypified. Descriptions, illustrations, distribution maps, and an identification key to all taxa are provided. All species except *S. altissima*, *S. angulata*, and *S. glaziovii* were studied in the field. Species of section *Neosymplocos* are distributed mainly in the Serra do Mar (Mata Atlântica rain forest) of southern and southeastern Brazil. Nearly 55% of them are narrow endemics, rare, and probably threatened with extinction through habitat destruction of their montane environments.

Resumo

Uma revisão taxonômica de *Symplocos* Jacq. seção *Neosymplocos* Brand é aqui fornecida para substituir o desatualizado 1901 tratamento de Brand. Um total de 780 exsicatas e 17 fotografias de 23 herbários foram examinadas para avaliar a importância taxonômica das características morfológicas. Onze espécies são reconhecidas (*S. altissima*, *S. angulata*, *S. corymboclados*, *S. falcata*, *S. glandulosomarginata*, *S. glaziovii*, *S. insolita*, *S. microstyla*, *S. nitidiflora*, *S. organensis*, e *S. tenuifolia*), um nome novo é proposto (*S. insolita*), e vários nomes foram lectotipificados. Descrições, ilustrações, mapas e uma chave de identificação para todos os táxons são aqui fornecidas. Todas as espécies exceto *S. altissima*, *S. angulata* e *S. glaziovii* foram estudadas no campo. Espécies da seção *Neosymplocos* são distribuídas principalmente na Serra do Mar (Mata Atlântica) do sul e sudeste do Brasil. Aproximadamente 55% delas são endêmicas restritas, raras e provavelmente ameaçadas de extinção devido a destruição de seus habitats montanos.

The family Symplocaceae [order Ericales *sensu* Angiosperm Phylogeny Group (1998, 2003)] comprises the single genus *Symplocos* Jacq. with ca. 325 species of woody flowering plants distributed in the tropical and subtropical regions of the Americas, southern and eastern Asia, Australia,

and the East Indies, with several species reaching the temperate zones of North America and Eastern Asia (Brand 1901; Wood and Channel 1960; Wang et al. 2004; Fritsch et al. 2006). *Symplocos* is recognized by alternate, simple, exstipulate leaves, axillary (rarely terminal), usually multi-flowered inflorescences, bisexual or rarely unisexual actinomorphic flowers, a connate calyx and corolla, an androecium with usually numerous epipetalous bi- or multiseriate or fasciculate stamens with globose to ellipsoid anther sacs, a two- to five-carpellate inferior ovary, an undivided style, one to four unitegmic ovules per locule, and a drupaceous fruit crowned by the persistent calyx (Nooteboom 1975; Cronquist 1981). Phylogenetic studies based on DNA sequence data strongly support Symplocaceae as monophyletic (Soejima and Nagamasu 2004; Wang et al. 2004; Fritsch et al. 2006).

Previous Systematic Work on *Symplocos* sect. *Neosymplocos*

The most recent and comprehensive published taxonomic treatment of *Symplocos* is that of Brand (1901). Brand recognized four subgenera within *Symplocos*: *Epigenia* (Vell.) Brand, *Eusymplocos* Brand (≡ subg. *Symplocos*), *Hopea* (L.f.) C.B. Clarke, and *Microsymplocos* Brand. Subgenus *Microsymplocos* comprises two sections disjunct between the Greater Antilles (section *Urbaniocharis* Brand) and southern and southeastern Brazil (section *Neosymplocos* Brand). According to Brand (1901), this subgenus is characterized by small flowers, monadelphous stamens, and claviform filaments. Species of section *Neosymplocos* are readily distinguished from those of section *Urbaniocharis* by their pubescent filaments (versus glabrous), a likely synapomorphy for the section (Aranha Filho et al. 2005). Brand (1901) described 11 species and one variety for section *Neosymplocos* (*S. aegrota*, *S. altissima*, *S. angulata*, *S. ascendens*, *S. corymboclados*, *S. densiflora* var. *densiflora*, *S. densiflora* var. *minor*, *S. falcata*, *S. glaziovii*, *S. nitidiflora*, *S. organensis*, and *S. tenuifolia*), all of which were newly described. Brand recognized three species in section *Urbaniocharis* (*S. ciponimoides* Griseb., *S. lanata* Krug et Urb., and *S. micrantha* Krug et Urb.), a section in which currently seven species are recognized (Fritsch and Almeda, in prep.).

Pollen morphology has been considered important in the infrageneric classification and phylogeny of *Symplocos*. Thus Nooteboom (1975), in his revision of *Symplocos* of the Old World, placed subgenus *Microsymplocos* under subgenus *Hopea* based largely on the palynological data of Meijden (1970). Meijden, however, did not have sufficient material of *Microsymplocos* for a critical study of subgenus *Microsymplocos*: only *S. lanata* (section *Urbaniocharis*) and *S. tenuifolia* (section *Neosymplocos*) were sampled.

Nagamasu (1989a, 1989b, 1993) concluded that the pollen of species in subgenus *Hopea* is structurally different from that of section *Neosymplocos*. Pollen grains of subgenus *Hopea* have a thin tectum, supratectal ornamentation, and a distinct columella layer (versus a massive tectum lacking supratectal ornamentation and an indistinct columella layer). Moreover, Barth (1979, 1982) and Nagamasu (1989a, 1989b, 1993) noted that pollen of the species of section *Neosymplocos* is similar to that of subgenus *Symplocos*. Based on these observations, Nagamasu (1989a, 1989b, 1993) recognized *Microsymplocos* at the subgeneric level, and suggested a close relationship between subgenera *Microsymplocos* and *Symplocos*.

Nagamasu, however, did not consider Mai's (1986) evidence that species of *Urbaniocharis* possess pollen similar to species of sections *Pseudosymplocos* Brand and *Barberina* (Vell.) A.DC. (both within subgenus *Epigenia*), which resemble the pollen types of subgenus *Hopea*. Thus, a massive tectum lacking supratectal ornamentation and an indistinct columella layer would be confined only to pollen of section *Neosymplocos* and subgenus *Symplocos*.

In their molecular phylogenetic studies of *Symplocos*, Wang et al. (2004) and Fritsch et al.

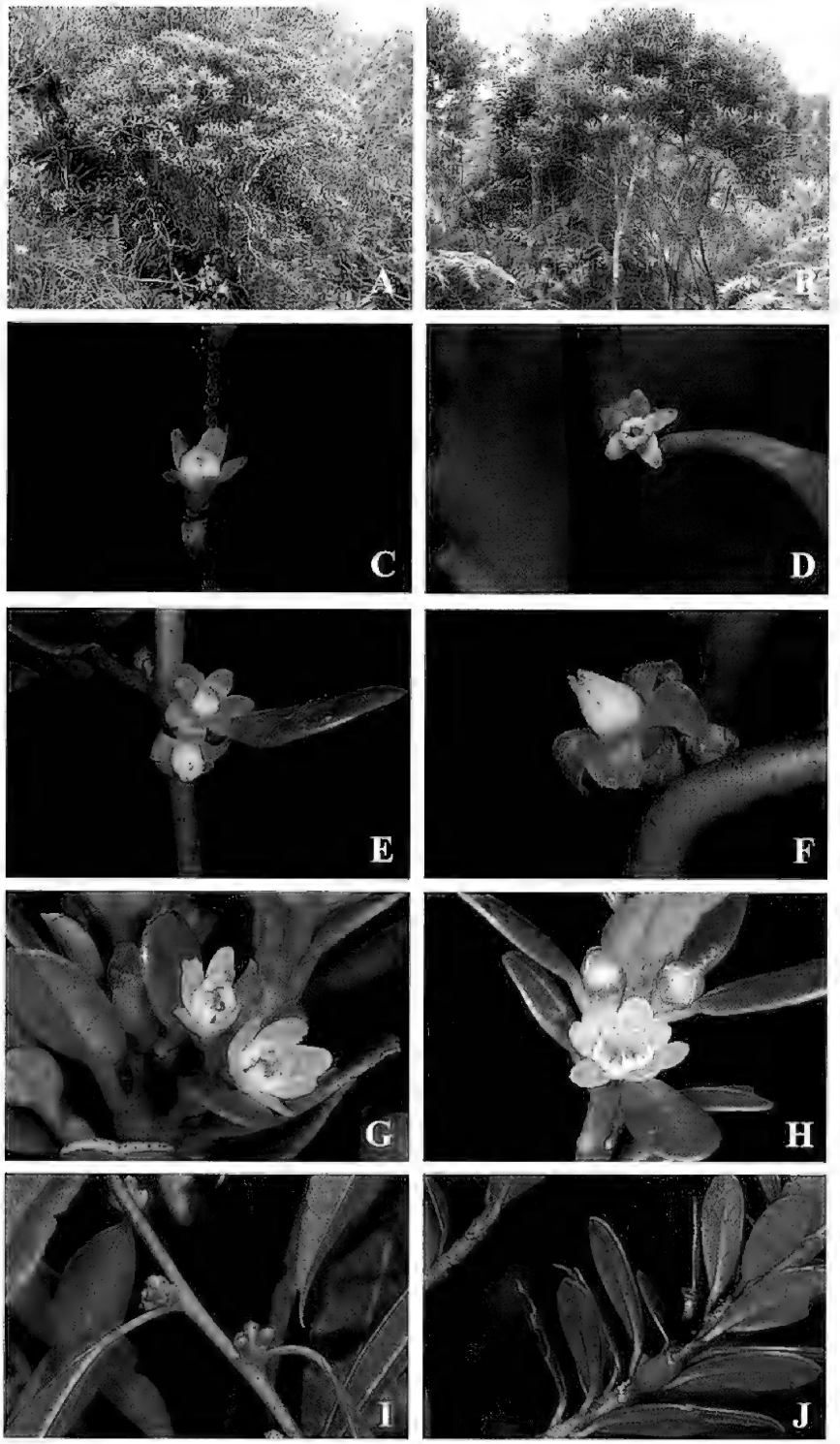

FIGURE 1. Photographs of some *Neosymplocos* Brand species. A. Habit of *S. corymboclados*; B. Habit of *S. glandulosomarginata*; C. Flower of *S. corymboclados*; D. Flower of *S. falcata*; E. Inflorescence of *S. nitidiflora*; F. Flower of *S. nitidiflora*; G. Flower of *S. organensis*; H. Flower of *S. organensis*; I. Immature fruits of *S. falcata*; J. Immature (green) and mature (blackish) fruits of *S. organensis*. (Photo A-B by P.W. Fritsch; D, G-J by F. Almeda; C, E-F by J.L.M. Aranha Filho).

(2006) concluded that although the two sections of subgenus *Microsymplocos* are monophyletic, subgenus *Microsymplocos* is not. Instead, section *Neosymplocos* nests within section *Symplocastrum* Brand of subgenus *Symplocos* and section *Urbaniocharis* is sister to the clade comprising sections *Symplocastrum* and *Neosymplocos*.

Upon closer inspection, the characters used by Brand (1901) to define subgenus *Microsymplocos* (other than the small flowers) appear to be based on erroneous observations. Species of section *Urbaniocharis* have indistinctly pentadelphous rather than strictly monadelphous stamens, and filamentous rather than clavate filaments (Fritsch and Almeda, in prep.). In contrast, species of section *Neosymplocos* possess monadelphous stamens and linear-deltoid filaments. These observations help to reconcile the polyphyly of subgenus *Microsymplocos* based on molecular evidence with Brand's circumscription of the subgenus. The small flower size of both sections is possibly a convergent adaptation for small pollinating insects (Borhidi 1996; Wang et al. 2004). Moreover, sections *Neosymplocos* and *Symplocastrum* share several floral characteristics in addition to the palynological ones already discussed. As observed in *Symplocos organensis* and *S. falcata*, the anthers sacs release pollen prior to anthesis. The same phenomenon has been observed in some species of *Symplocastrum* from Mesoamerica (R. Kriebel, pers. comm.). Also, species of both sections have monadelphous stamens and flattened filaments (versus terete filaments in section *Urbaniocharis*).

According to Kelly and Almeda (2002), Brand's monograph is clearly outdated. Recent phylogenetic studies (Soejima and Nagamasu 2004; Wang et al. 2004; Fritsch et al. 2006) provide a sound basis for a new infrageneric classification. Wang et al. (2004) noted the relative lack of taxonomic and morphological studies on section *Neosymplocos*; most published research involving species of this section has been restricted to new species descriptions and treatments in regional floras (e.g., Sleumer 1937; Hoehne 1938; Occhioni 1974, 1975a, 1975b; Aranha Filho et al. 2005). An unpublished taxonomic revision of the group was presented as part of a Ph.D. dissertation (Bidá 1995). This work, although in many ways an improvement over Brand's treatment, in our view contains questionable species circumscriptions and an inadequate key to species, among other problems. Here we provide a taxonomic revision of *Symplocos* section *Neosymplocos* based on detailed comparative morphological data to update Brand's treatment.

Geographic Distribution, Endemism, and Habitat of the Species of *Symplocos* sect. *Neosymplocos*

The 11 species recognized in this treatment are nearly endemic to Brazil; only *Symplocos tenuifolia* reaches Paraguay (Bidá 1995). Species of *Neosymplocos* are found primarily in montane habitats of the Serra do Mar (Mata Atlântica rain forest) of southern and southeastern Brazil (although there are no species known from Rio Grande do Sul). Species are to be expected in the Mata Atlântica of northeastern Brazil (especially Bahia) when the Brazilian highland flora becomes better documented. Only three species (*S. insolita*, *S. microstyla*, and reportedly *S. angulata*) occur in "campo rupestre" (rocky field) habitats, all in the southern portions of the Cadeia do Espinhaço.

Symplocos falcata, *S. glandulosomarginata*, and *S. tenuifolia* are the most geographically widespread and common (i.e., collections from many localities); *S. corymboclados* and S. *nitidiflora* are also geographically widespread but uncommon. The other species are rare and appear to be narrowly endemic. *Symplocos altissima*, *S. glaziovii* (both restricted to the Serra dos Órgãos in Rio de Janeiro state), and *S. angulata* (restricted to the Serra do Caraça in Minas Gerais) were collected only prior to 1900. *Symplocos organensis* is endemic to Rio de Janeiro and apparently restricted to montane elfin forest in the Serra dos Órgãos. *Symplocos insolita* and *S. microstyla* are endemic to the Serra do Cipó and Serra do Caraça (both in Minas Gerais), respectively. Thus, six out of

11 species (54.5%) are narrow endemics.

Most species of *Symplocos* section *Neosymplocos* occur exclusively from 1000 to 2000 m elevation (*S. corymboclados*, *S. insolita*, *S. microstyla*, *S. organensis*, and reportedly *S. altissima*, *S. angulata*, and *S. glaziovii*). Some species, however, are also found at lower elevations of the Mata Atlântica (*S. falcata*, *S. glandulosomarginata*, *S. nitidiflora*, and *S. tenuifolia*). There are no species occurring exclusively in the lowlands of the Mata Atlântica.

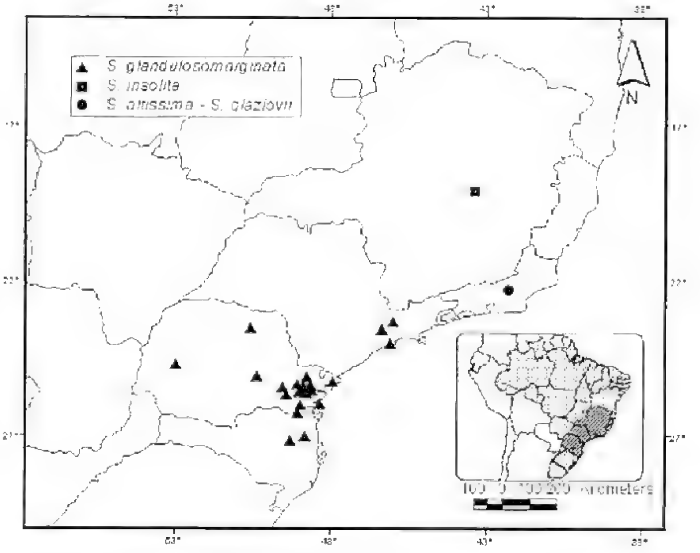

FIGURE 2. Distribution of *Symplocos altissima*, *S. glandulosomarginata*, *S. glaziovii*, and *S. insolita*.

Most *Neosymplocos* species grow in a limited range of habitats within the Mata Atlântica, occurring mainly in elfin forest and montane ombrophilous forest. Only the widespread and fairly common species are found in additional habitats, such as araucaria forest, riparian situations, secondary and semideciduous forests, and even "restinga" (a coastal sand community of eastern Brazil with low nutrient status and high insolation). *Symplocos insolita*, *S. microstyla*, and reportedly *S. angulata* are found in campo rupestre.

MATERIALS AND METHODS

Type material and general collections from the following herbaria were studied: BM, BHCB, CAS, ESA, G, GUA, HB, HRCB, IAC, K, M, MBM, NY, R, RB, RFA, S, SP, SPF, SJRP, UEC, and UPCB. The collections from B were examined through the internet as digital photographs. A total of 17 photographic images and nearly 780 specimens, including the types of all names involved in this treatment except *S. corymboclados* var. *micromorpha*, were examined. Field work during November, 2004 (São Paulo, Minas Gerais, and Rio de Janeiro) and October, 2005 (Minas Gerais and Paraná) supplemented the study of herbarium specimens. An index to specimens studied, a comparison of our revision to those of Brand (1901) and Bidá (1995), and a list of scientific names in this work are provided in Appendices 1, 2, and 3, respectively.

Several specimens that could be considered types presented discrepancies concerning collection data (e.g., identical collection numbers but different dates, different localities). This is especially true of collections ascribed to A.F.M. Glaziou, data from which are known to be unreliable or confusing (Wurdack 1970). Brand (1901) mentioned no date in the protologue of the names attached to these types, which would otherwise have helped to guide assessments of typification. In many cases, we assumed that these discrepancies are transcription errors or errors in matching the label information to the specimen. Some specimens nonetheless have been tentatively excluded from the type collection cited here, even when collector and number matched the type collection, because the localities on their labels did not match those cited by Brand (1901) in the protologue. Comments on such specimens are provided in the species discussion sections. When no locality was

provided, we assumed that the specimen is a type. The dates provided in the typification are derived from the labels of designated lectotypes.

All descriptions are based on field observations and herbarium specimens. The habit of *Symplocos altissima*, *S. angulata*, and *S. glaziovii* and corolla lobe color of *S. angulata* and *S. glaziovii* were taken from the original descriptions. Flowering and fruiting periods, vernacular names, elevational ranges, distribution, habit, and habitat were based on label information of herbarium specimens and field observations. Specimens without precise geographic coordinates (nearly all) were estimated from label information as supplemented by data from maps and on-line gazetteers (*http://www.biolink.csiro.au/gazfiles.html; http://gnswww.mil/geonames/gns/index.jsp*). Some characters used in the descriptions and keys, such as anther color and corolla lobe posture, are based on field observations.

Some species known to us only from the type collection (*Symplocos altissima*, *S. angulata*, and *S. glaziovii*) had few open flowers that were difficult to measure without damage to the specimen, or only had flower buds. In these cases, flower length was measured from the largest available bud on the specimen. The hypanthium was measured from the floral articulation to the base of the calyx lobes. Corolla lobe and stamen measurements were taken from dissected flowers at anthesis whenever possible. Stamen length was measured from the base of the distinct portions of the filaments to the apex of the anthers. Corolla lobe width was measured at the widest point. *Symplocos altissima*, *S. angulata*, and *S. glaziovii* were poorly sampled due the scarce material available and the lack of flowers at anthesis. In these cases, we measured the corolla lobes, stamens, disc, and style of the largest flowers found on available specimens. Fruit length was measured at maturity and included the height of the calyx lobes or the disc.

Taxonomic Treatment

Symplocos sect. ***Neosymplocos*** Brand in Engl., Pflanzenr. IV. 242 (6):70. 1901.

Type.— *Symplocos tenuifolia*.

Evergreen tree or shrub, occasionally candelabriform, usually densely branched from middle upward. Branches emerging at a 45° angle, mature branches various shades of brown, commonly striate longitudinally. Petiole adaxially concave, flattened, or canaliculate, abaxially ± rounded; leaf blade drying green to brown, rotund to spatulate, coriaceous, venation ± brochidodromous, midvein sulcate adaxially, secondary and tertiary veins branched near both midvein and margin, margin revolute, marginal glands usually present at least distally and frequently caducous, apical gland often present and early caducous or rarely persistent. Inflorescence axillary, fasciculate, 1- to 20-flowered; bracts usually numerous, basal two commonly early caducous, others persistent, margin ciliate, apex acute to rounded. Flower bisexual, actinomorphic, sessile, articulate, 1.5–11 mm long; hypanthium glabrous or rarely strigillose; calyx lobes 5, erect, deltoid to rotund, margin ciliate; corolla lobes 5 to 8, elliptic to rotund, usually glabrous, margin ciliate. Stamens 20 to 40, monadelphous, indistinctly 2- to 5-seriate, arched inwardly, connate, adnate to corolla, frequently exceeding gynoecium; filaments white, linear-deltoid, flattened tangentially, occasionally constricted at apex, subfleshy, pubescent; anthers white, greenish white, or yellow, latrorse, ellipsoid becoming globose upon dehiscence. Ovary inferior, 3(4)-locular; disc flat or prominently elevated, smooth to rugose; style straight, terete, glabrous or rarely sparsely pubescent; stigma 3(4)-lobed; ovules 2 per carpel, ± ovoid. Drupe (1)2(3)-locular, green when immature and black when mature, ellipsoid to globose, disc not reaching or rarely exceeding persistent calyx lobes; calyx lobes erect to tightly appressed to disc. Seed 1(to 3) per fruit. Embryo straight; cotyledons longer than the radicle.

Key to Species of *Symplocos* sect. *Neosymplocos*

Asterisks (*) denote species that fall out twice in the key.

1a. Disc prominently elevated (0.7–1 mm).
  2a. Candelabriform shrub; young leaf blade abaxially strigose; base of leaf blade cordate or subcordate; fruit 3–5 mm wide . . . . . 7. *S. insolita*
  2b. Small tree (reportedly); young leaf blade abaxially tomentose; base of leaf blade cuneate, rounded, or subrounded; fruit 5–7 mm wide . . . . . 2. *S. angulata*
1b. Disc flat.
  3a. Margin of mature leaf blade with 13 to 25 glands per cm . . . . . 5. *S. glandulosomarginata*
  3b. Margin of mature leaf blade with 0 to 8 glands per cm.
    4a. Young leaf blade abaxially glabrous.
      5a. Leaf blade 8–11 × 4–5.5 cm; the two basal bracts rotund to subrotund, 3–4 × 1.5–2.5 mm; calyx and corolla lobes densely strigillose abaxially . . 1. *S. altissima*
      5b. Leaf blade 2–6.5 × 0.5–2.5 cm; the two basal bracts deltoid or subdeltoid, 0.5–2 × 0.4–1.5 mm; calyx and corolla lobes glabrous or sparsely pubescent abaxial-medially.
        6a. The two basal bracts 0.5–1 × 0.4–0.7 mm; flower 2–4 mm long; calyx lobes 1–1.5 × 0.8–1 mm; corolla lobes 1.5–2.5 mm long; anthers white or greenish white; fruit 5–7 × 3–5 mm . . . . . 3. *S. corymboclados**
        6b. The two basal bracts 1.5–2 × 1–1.5 mm; flower 4–11 mm long; calyx lobes 1.5–2 × 1–1.5 mm; corolla lobes 2.7–3.5 mm long; anthers yellow; fruit 7–12 × 5–7 mm . . . . . 10. *S. organensis*
    4b. Young leaf blade abaxially pubescent.
      7a. Young leaf blade strictly tomentose abaxially; leaf blade 0.5–4 × 0.3–1.6 cm.
        8a. Young leaf blade eglandular; leaf blade elliptic, oblong, obovate, ovate, or rotund; hypanthium 0.4–0.5 mm long; calyx lobes 0.5–1 mm long; style ca. 0.1 mm long . . . . . 8. *S. microstyla*
        8b. Young leaf blade glandular; leaf blade oblanceolate or spatulate; hypanthium 0.8–1.1 mm long; calyx lobes 1–1.2 mm long; style 0.4–0.6 mm long . . . . . 6. *S. glaziovii*
      7b. Young leaf blade strigose, strigillose, sericeous-strigose, or mixed tomentose-pilose-sericeous abaxially, if strictly tomentose then leaf blade 5–16 × 1.8–4 cm.
        9a. The two basal bracts 3–4 × 1.3–2.5 mm; hypanthium densely strigillose or rarely glabrous; corolla lobes 2.2–3.5 mm wide, reflexed; anthers yellow; style 1–1.5 mm long; fruit 10–20 mm long . . . . . 9. *S. nitidiflora*
        9b. The two basal bracts 0.7–3 × 0.5–1.5 mm; hypanthium glabrous; corolla lobes 1–2 mm wide, ascending or spreading (unknown in *S. tenuifolia*); anthers white to green (unknown in *S. tenuifolia*); style 0.5–1 mm long; fruit 3–10 mm long.
          10a. Young leaf blade abaxially mainly tomentose near margin, otherwise sericeous-pilose, adaxially densely sericeous or pilose along midvein; calyx lobes glabrous or rarely sparsely pubescent abaxial-medially; fruit 3–6 mm long, ovoid or globose . . . . . 11. *S. tenuifolia*
          10b. Young leaf blade abaxially sericeous-tomentose or strigose throughout, adaxially glabrous or rarely puberulent on basal half of midvein, or if densely sericeous or tomentose along midvein then calyx lobes densely

sericeous-tomentose or strigose abaxially and fruit 8–10 mm long, cylindrical or nearly so.

11a. Young leaf blade glabrous adaxially; leaf blade 2–6.5 × 0.8–2.5 cm; calyx lobes glabrous or sparsely pubescent abaxially, then glabrescent; fruit 5–7 mm long ..... 3. *S. corymboclados**

11b. Young leaf blade sericeous-tomentose or sericeous-strigose adaxially, rarely glabrous; leaf blade 5–16 × 1.8–4 cm; calyx lobes densely pubescent abaxially, rarely glabrescent; fruit 8–10 mm long ..... 4. *S. falcata*

1. Symplocos altissima Brand in Engl., Pflanzenr. IV. 242 (6):71. 1901. TYPE.— BRAZIL. Rio de Janeiro: "Alto do Macahé bei Nova Friburgo" (protologue), 1892, *A.F.M. Glaziou 19618* (holotype: B destroyed; photo of holotype: NY!, RFA!; lectotype, here designated: K!; isolectotypes: IAN, P).

The B holotype of *Symplocos altissima* was destroyed during World War II. The only type material we have seen is that from K, which we therefore designate as lectotype.

Reportedly a tall tree. Branches distally flattened, smooth, glabrous. Petiole 5–15 mm long, adaxially concave, glabrous; leaf blade broadly elliptic or occasionally ovate or obovate, 8–11 × 4–5.5 cm, glabrous, base attenuate or cuneate, margin conspicuously serrate on distal ¾ or occasionally serrulate or crenate, marginal and apical glands usually early caducous, persistent glands 0 to 8 per cm, apex acuminate or occasionally broadly obtuse, acumen (when present) 1–3 mm long. Inflorescence 4–10 mm long, 1- to 8-flowered; bracts 7 to numerous, densely ferrugineous-strigillose abaxially, margin ciliate; the two basal bracts caducous, rotund to subrotund, keeled to concave, 3–4 × 1.5–2.5 mm, apex rounded, apical gland usually lacking; other bracts 1–2 × 1–2 mm, apices of basalmost rounded, gradually more acute distally. Flower 3–6 mm long; hypanthium 1–1.5 mm long, glabrous; calyx lobes deltoid to subdeltoid, 1–1.5 × 0.8–1 mm, densely golden yellow- to ferrugineous-strigillose abaxially; corolla lobes 5(6), elliptic to subrotund, 3–5 × 2–3 mm, densely golden yellow- to ferrugineous-strigillose abaxially. Stamens 25 to 30(to 35), exceeding and obscuring gynoecium; filaments 0.5–3 mm long. Disc 1–1.5 mm in diameter, flat, rugose, glabrous or sparsely pubescent; style 1–1.5 mm long, glabrous or rarely sparsely pubescent. Fruit unknown.

VERNACULAR NAME.— None.

ILLUSTRATION.— Figure 3.

PHENOLOGY.— Unknown.

DISTRIBUTION AND HABITAT.— Endemic to Nova Friburgo (Rio de Janeiro). Reportedly in elfin forest at ca. 2000 m elevation in the Serra dos Órgãos (Bidá 1995) but species of *Neosymplocos* that occur in such forests usually have smaller leaves (e.g., *Symplocos organensis*). It is therefore possible that *S. altissima* occurs in the lower montane ombrophilous forest of Nova Friburgo. Distribution map, Figure 2.

DISCUSSION.— *Symplocos altissima* is recognized by its glabrous leaves and calyx and corolla lobes that are densely strigillose abaxially. *Symplocos nitidiflora* and usually *S. falcata* are the only other species of section *Neosymplocos* with densely strigillose calyx and corolla lobes. The leaves of the last two species, however, are pubescent at least when young, whereas those of *S. altissima* are glabrous.

ADDITIONAL SPECIMEN EXAMINED.— BRAZIL. No location indicated, *A.F.M. Glaziou* (illegible number) (BM).

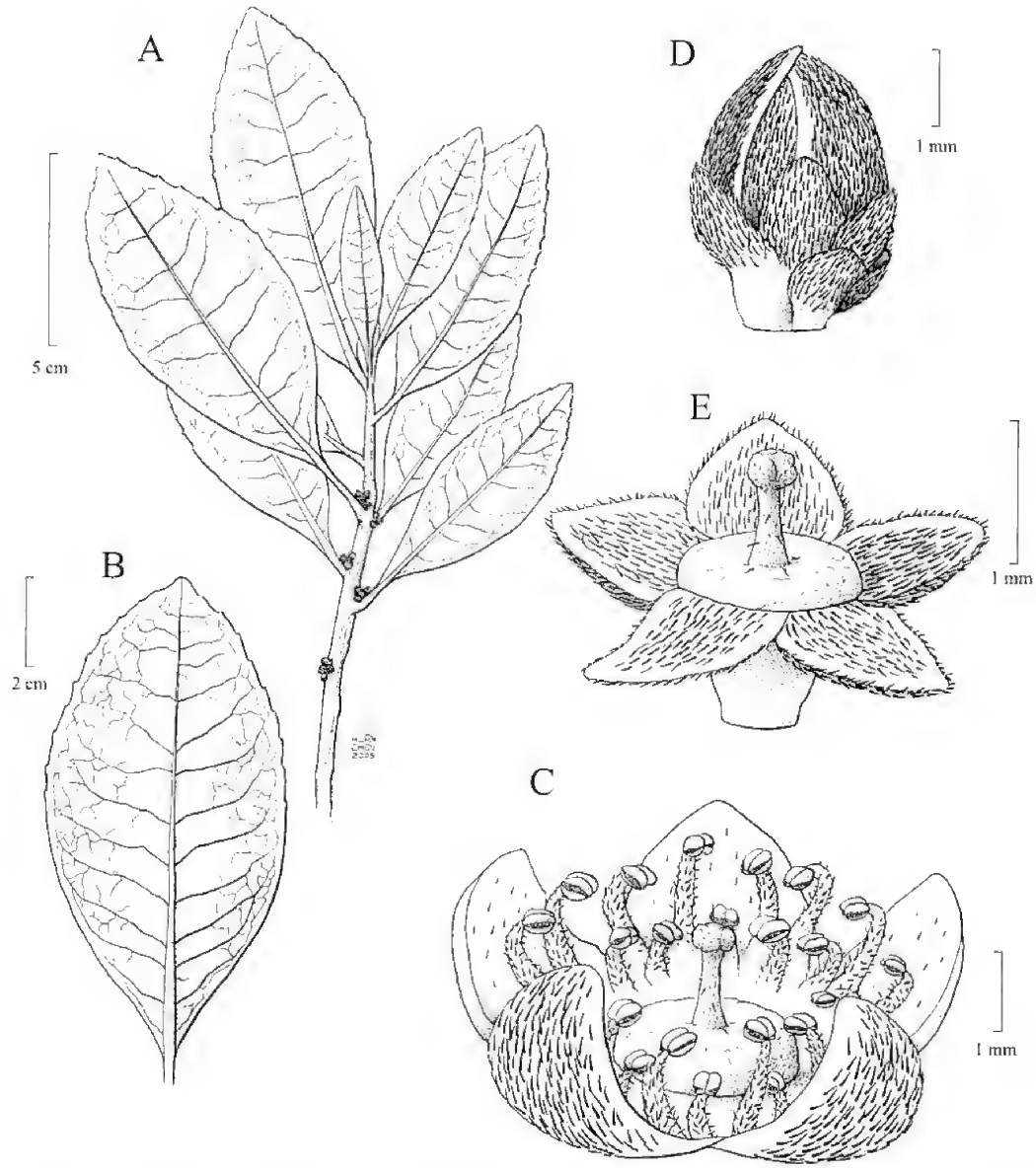

FIGURE 3. *Symplocos altissima* Brand. A. Flowering branch; B. Representative leaf (abaxial surface); C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud and subtending bract; E. Flower with corolla and androecium removed. (A–E from *Glaziou 19618*).

2. Symplocos angulata Brand in Engl., Das Pflanzenreich IV. 242 (6):73. 1901. TYPE.—BRAZIL. Minas Gerais: Serra do Caraça, Morro do Inficcionado, 1885, *A.F.M. Glaziou 15189* (holotype: B destroyed; photo of holotype: NY!; lectotype, here designated: G!; isolectotypes: K!, P (3)).

Symplocos angulata was described by Brand (1901) from *Claussen 174* and *Glaziou 15189*. *Glaziou 15189* is the only collection seen by the authors. We selected the specimen at G as lectotype because its label has the same locality provided by Brand (1901) in the protologue. In addition, it has fruiting and flowering material.

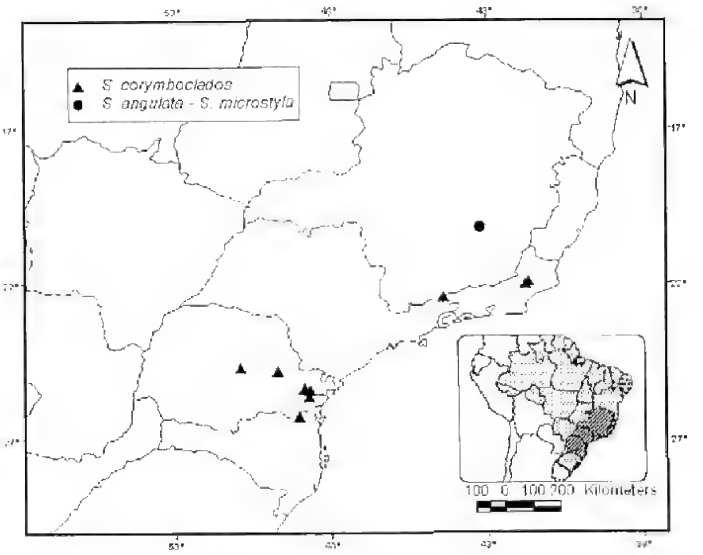

FIGURE 4. Distribution of *Symplocos angulata*, *S. corymbosclados*, and *S. microstyla*.

Reportedly a small tree. Branches strongly angled, striate, fissured, tawny tomentose, glabrescent. Petiole 1–3 mm long, adaxially flat, tawny tomentose, glabrescent; leaf blade obovate or occasionally rotund, broadly oblong or ovate, 2.5–4.7 × 1.5–3 cm, abaxially densely tawny tomentose, rarely glabrescent, adaxially sparsely puberulent on basal half of midvein, otherwise glabrous, glabrescent, secondary and tertiary veins sparsely branched near midvein and margin, base cuneate or occasionally rounded to subrounded, margin entire or occasionally inconspicuously serrulate mainly on distal half, marginal and apical glands usually early caducous, persistent glands 0 to 8 per cm, apex obtuse, retuse, or rarely truncate. Inflorescence 4–8 mm long, 1- to 5-flowered; bracts 7 to 15(to 20), margin ciliate; the two basal bracts caducous, rotund to subrotund, keeled, 1.5–2 × 1–1.5 mm, densely to sparsely tawny tomentose abaxially, apex rounded or nearly so, apical gland usually lacking; other bracts 1–2 × 1–2 mm, glabrous or rarely sparsely tawny tomentose abaxial-medially, apices of basalmost subobtuse to obtuse, gradually more acute distally. Flower 3–6 mm long; hypanthium 1–1.5 mm long, glabrous; calyx lobes deltoid to occasionally rotund, 1–2 × 1–2 mm, glabrous or rarely sparsely tawny tomentose abaxially and then glabrescent; corolla lobes 5, reportedly pink, obovate to subrotund, 2–5 × 1.5–3 mm, glabrous or rarely sparsely pubescent, margin ciliate. Stamens 25 to 35, exceeding and obscuring gynoecium; filaments 0.5–2 mm long. Disc 0.8–1 mm in diameter, prominently elevated (0.7–1 mm), rugose, glabrous; style 0.5–1 mm long, glabrous. Fruit 2(3)-locular, 7–9 × 5–7 mm, disc not enlarged and not distended beyond persistent calyx; calyx lobes erect to slightly appressed to disc, glabrous. Seed 1, 3–5 × 1.5–2 mm.

VERNACULAR NAME.— None.

ILLUSTRATION.— Figure 5.

PHENOLOGY.— Flowering in June; fruiting in March and June.

DISTRIBUTION AND HABITAT.— Endemic to the Serra do Caraça, Pico do Inficcionado, in the southern part of the Cadeia do Espinhaço (Minas Gerais) reportedly in campo rupestre. Our field work on Pico do Inficcionado during October, 2005 failed to relocate this species in its natural habitat. Distribution map, Figure 4.

DISCUSSION.— *Symplocos angulata* is distinguished by the combination of its cuneate, subrounded, or rounded leaf base, tomentose young leaves abaxially, and prominently elevated (0.7 to 1 mm) disc. *Symplocos insolita*, the only other species of *Neosymplocos* that has an elevated disc, can be distinguished from *S. angulata* by the characters in the key.

ADDITIONAL SPECIMENS EXAMINED.— **BRAZIL. Minas Gerais:** Serra do Caraça, Mar. 1892, *E.H.G. Ule 2475* (R). No location indicated, 1842, *P. Claussen 200* (BM).

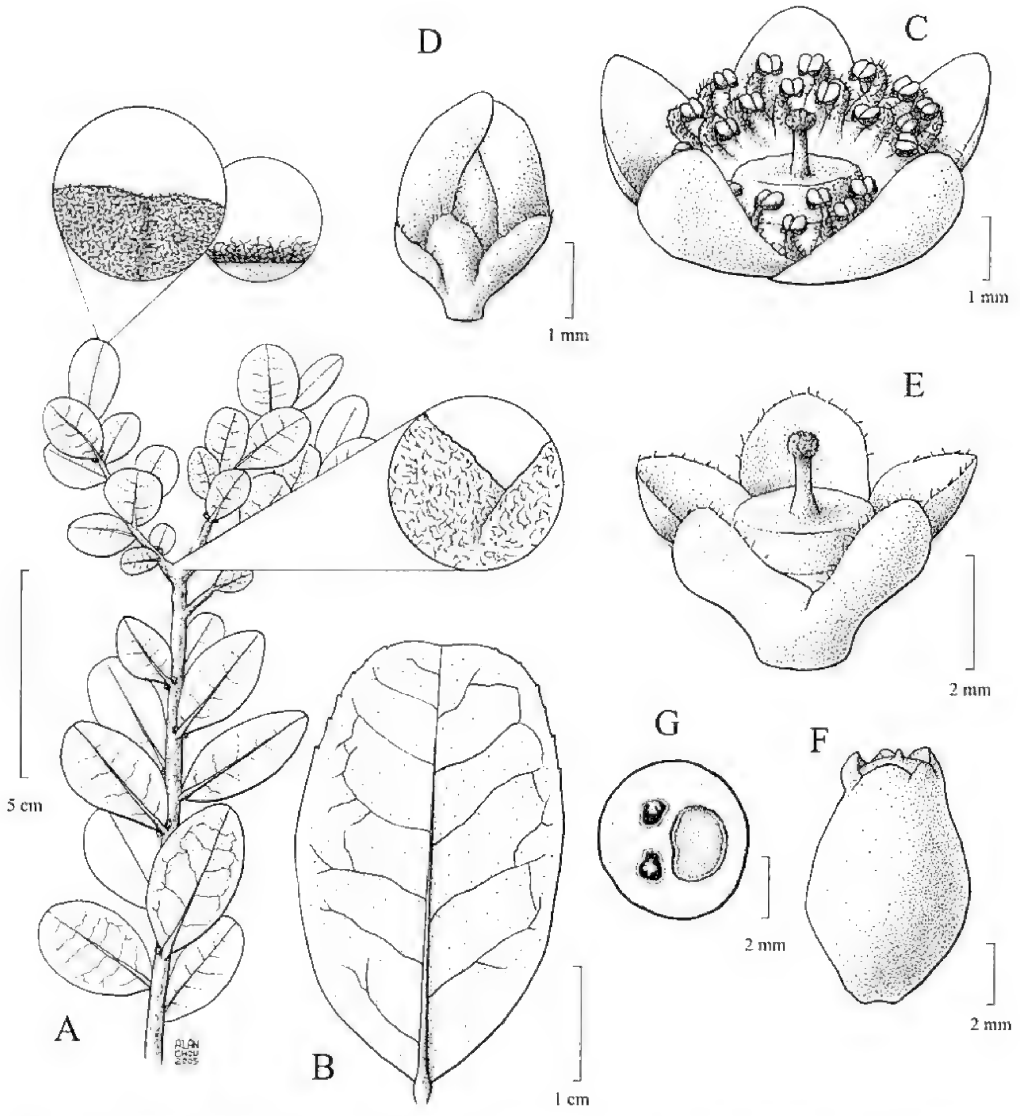

FIGURE 5. *Symplocos angulata* Brand. A. Flowering branch with branch and leaf indument detail; B. Representative leaf (abaxial surface); C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud. E. Flower with corolla and androecium removed; F. Mature fruit; G. Mature fruit in cross-section. (A–B from *Claussen 200*; C–G from *Glaziou 15189*).

3. Symplocos corymboclados Brand in Engl., Pflanzenr. IV. 242 (6):72. 1901. TYPE.— BRAZIL. Rio de Janeiro: "Alto do Macahé bei Nova Friburgo" (protologue), 1891, *A.F.M. Glaziou 18359* (holotype: B destroyed; photo of holotype: NY!, RFA!; lectotype, here designated: K!; isolectotypes: BR, P).

Symplocos corymboclados Brand var. *micromorpha* Sleumer, Repert. Spec. Nov. Regni Veg. 42. 264. 1937. TYPE.— BRAZIL. "In regionis silvaticae partibus superioribus montis Itatiaia, 1400–2000 m.s.m." (protologue), September 1901, *R. Wettstein & V. Schiffner s.n.* (holotype: B destroyed).

We examined *Glaziou 18359* from G and K, and two photographs of the destroyed B holotype from NY and RFA. We excluded the G specimen of *Glaziou 18359* from the type collection because the locality on its

label does not agree with that in the protologue. We therefore have designated the K specimen as lectotype because it is the only type material that we have seen.

No authentic material of *Symplocos corymboclados* var. *micromorpha* has been located. The description indicates that the only differences between the nominate variety and variety *micromorpha* are the leaf dimensions. The leaves of the nominate variety are 2–6.5 × 0.8–2.5 cm and those of variety *micromorpha* are 3–3.5 × 0.8–1 cm. These differences are insignificant and unworthy of formal recognition at the infraspecific level.

Shrub or tree 1–10 m tall. Branches ± terete, striate, fissured, glabrous or white- or golden yellow-strigose, then glabrescent. Petiole 5–8 mm long, adaxially concave to canaliculate, glabrous or white- or golden-yellow-strigose, then glabrescent; leaf blade elliptic to obovate, 2–6.5 × 0.8–2.5 cm, abaxially glabrous to densely white- or golden yellow-strigose, then glabrescent, adaxially glabrous or rarely puberulent on basal half of midvein, then glabrescent, secondary and tertiary veins highly branched near midvein and margin, base attenuate to cuneate, margin inconspicuously serrulate on distal half, rarely conspicuously serrate, marginal and apical glands usually early caducous, persistent glands 0 to 8 per cm, apex acuminate or nearly acute, acumen (when present) 1–7 mm long. Inflorescence 5–8 mm long, 1- to 6-flowered; bracts 7 to 25, glabrous or abaxially sparsely white- or golden yellow-strigillose mainly along medial vein, margin frequently ciliate; the two basal bracts usually early caducous, deltoid, keeled to concave, 0.5–1 × 0.4–0.7 mm, apex acute or nearly so, apical gland usually lacking; other bracts 1–2 × 1–2 mm, apices of basalmost obtuse, gradually more acute distally. Flower 2–4 mm long; hypanthium 0.8–1.3 mm long, glabrous; calyx lobes nearly deltoid to rotund, 1–1.5 × 0.8–1 mm, glabrous or sparsely white- or golden yellow-strigillose abaxial-medially and then glabrescent; corolla lobes 5(6), ascending, white, cream, or green, elliptic to subrotund, 1.5–2.5 × 1–2 mm, glabrous or sparsely white- or golden yellow-strigillose abaxial-medially. Stamens 20 to 35(to 40), exceeding and obscuring gynoecium; filaments 0.5–1.5 mm long; anthers white or greenish white. Disc 0.5–1 mm in diameter, flat, smooth or ± rugose, glabrous or rarely sparsely pubescent; style 0.5–1 mm long, glabrous. Fruit 1(2 or 3)-locular, ellipsoid or cylindrical, 5–7 × 3–5 mm, disc not enlarged and not distended beyond persistent calyx; calyx lobes erect or slightly appressed to disc, glabrous. Seed 1(2 or 3), 4–5 × 2.5–3.3 mm.

Vernacular name.— congonha (*P. Campos Porto 831* (R, RB)).

Illustration.— Figure 6.

Photographic images.— Figures 1A, 1C.

Phenology.— Flowering usually from September to November, occasionally July and August; fruiting usually from November to March, occasionally in June or October.

Distribution and habitat.— *Symplocos corymboclados* is known from southeastern (Rio de Janeiro and Minas Gerais) and southern (Paraná and Santa Catarina) Brazil. In Rio de Janeiro it is disjunct between the northern and southern regions growing in windy, humid elfin forest between 1400 m to 1800 m elevation as a shrub or small tree although it is to be expected in high montane ombrophilous forest as well. It also occurs in the western part of the Serra do Itatiaia in Minas Gerais. In southern Brazil it grows in elfin forest (1100 m to 2000 m elevation) and high montane ombrophilous forest (1400 to 1850 m elevation) as a mid-canopy tree (ca. 10 m tall), and occasionally in riparian situations. In Paraná the species is widespread but uncommon. It occurs mainly in the Serra do Mar extending to the western region of Paraná in low montane ombrophilous forest. The species rarely occurs in secondary vegetation. Distribution map, Figure 4.

Discussion.— *Symplocos corymboclados* is characterized by the combination of its glabrous leaf blade adaxially (rarely puberulent along basal half of midvein), glabrous or (when young) strigose leaf blade abaxially, glabrous or sparsely pubescent calyx lobes, glabrous or medially pubescent corolla lobes abaxially, white to greenish white anthers, and fruit 5–7 mm long. It resem-

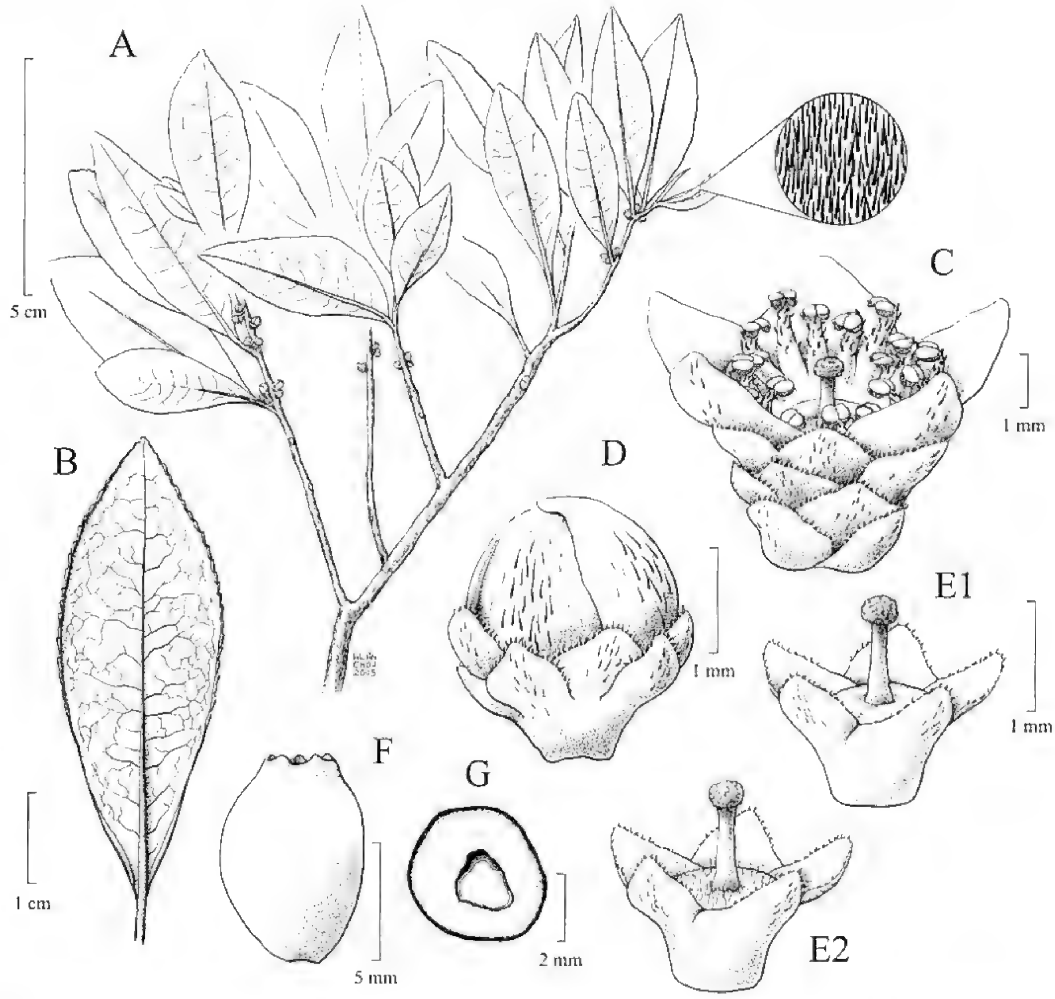

FIGURE 6. *Symplocos corymboclados* Brand. A. Flowering branch with leaf indument detail; B. Representative leaf (abaxial surface); C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud and subtending bracts; E1 and E2. Flower with corolla and androecium removed to show disc surface variation; F. mature fruit; G. Mature fruit in cross-section. (A–E1 from *Glaziou 18359*; E2 from *Hatschbach 17316*; F–G from *Lobão et al. 667*).

bles *S. falcata* in leaf shape, margin, and anther color. *Symplocos falcata*, however, has calyx lobes that are densely sericeous-tomentose or strigillose and fruit that is 8–10 mm long and calyx lobes with indument at least when young.

Individuals from Rio de Janeiro, Paraná, and a few from Santa Catarina generally differ in some morphological features. Specimens from Rio de Janeiro have secondary and tertiary veins impressed adaxially, leaves densely strigose abaxially with margin conspicuously serrate, corolla lobes frequently glabrous, and fruit ± ellipsoid with erect calyx lobes. In contrast, specimens from Paraná have glabrous or sparsely (rarely densely) strigose leaves abaxially, leaves with the secondary and tertiary veins impressed adaxially, a sparsely serrulate leaf blade margin, corolla lobes that are usually pubescent abaxial-medially, and a ± cylindrical fruit with calyx lobes slightly appressed to the disc. Several specimens from Santa Catarina are similar to those from Rio de Janeiro in their

pubescent leaf blade margin and glabrous corolla lobes. The secondary and tertiary veins, however, are strongly sulcate adaxially. We consider these morphological differences to be taxonomically insignificant because of strong overlap among populations from Rio de Janeiro and Paraná.

Based on morphological differences between specimens from Rio de Janeiro and Paraná, Bidá (1995) considered the Paraná collections as *S. hatschbachii* (ined.). We consider the Paraná material to represent variation within *S. corymboclados*, in agreement with Occhioni (1974).

ADDITIONAL SPECIMENS EXAMINED.— BRAZIL. **Minas Gerais:** Itatiaia, 1918, *P. Campos Porto 831* (R, RB). **Paraná:** Antonina, trail to Pico Caratuva, 19 Oct. 2005, *P.W. Fritsch et al. 1831* (CAS, MBM, UEC); Serra Ibitiraquire, Pico Paraná, 20 Dec. 1977, *O.S. Ribas & V.A.O. Dittrich 2185* (MBM, NY); Campina Grande do Sul, Morro Itapiroca, Kielse farm, 18 Sep. 1999, *E. Barbosa et al. 376* (MBM); Serra Ibitiraquire, 30 Nov. 1996, *J. Cordeiro & O.S. Ribas 1388* (B, BHCB, G, HRCB, MBM (2), NY); Serra do Ibitiraquire, Morro Tucum, 24 Oct. 2000, *J. Cordeiro et al. 1777* (MBM, RB); Pico Caratuva, 5 Oct. 1967, *G. Hatschbach s.n.* (B 100158489, HB 58575, MBM 23454); road to Rio Taquari-Rio Divisa, 18 Oct. 1959, *G. Hatschbach 6405* (G, MBM, RFA); Serra do Mar, Pico Caratuva, 5 Oct. 1967, *G. Hatschbach 17316* (BM, MBM, NY, RFA, S, UPCB); Pico Caratuva, 2 Aug. 1967, *G. Hatschbach 16836* (MBM); Serra de Ibitiraquire, 25 Sep. 1969, *G. Hatschbach 22230* (HB, MBM, RFA (2)); Serra Ibitiraquire, Pico Ferraria, 1 Nov. 2001, *A.Y. Mocochinski & M.B. Scheer 86* (MBM); Morro Tucum, 22 Dec. 1999, *O.S. Ribas et al. 2880* (MBM, SPF); Serra dos Órgãos, Pico Caratuva, 4 July 1991, *C.V. Roderjan & A. Vicentini 930* (MBM); Serra do Ibitiraquire, Pico Caratuva, 28 June 2002, *M.B. Scheer & A.Y. Mocochinski 451* (UPCB); Pico Paraná, Abrigo 3, 7 Sep. 1996, *J.M. Silva et al. 1696* (MBM, UPCB); trail to Pico Paraná, Serra Ibitiraquire, 5 Oct. 1997, *J.M. Silva et al. 2055* (MBM); Guaratuba, Serra do Araçatuba, Morro dos Perdidos, 18 Sep. 1997, *H.M. Fernandes & E.P. Santos 35* (MBM); Serra do Araçatuba, 15 Sep. 1982, *R. Kummrow 2033* (MBM); Serra do Araçatuba, Morro dos Perdidos, 18 Sep. 1997, *E.P. Santos & H.M. Fernandes 348* (MBM); Serra do Araçatuba, 23 Nov. 1996, *E.P. Santos et al. 284* (MBM, UPCB); Serra do Araçatuba, 15 Sep. 1995, *J.M. Silva & E.P. Santos 1053* (MBM); Laranjeiras do Sul, Rio Reserva, 18 Mar. 1987, *J.C. Lindeman & J.H. de Haas 5017* (MBM); Morretes, Serra da Prata, near Torre da Prata, 8 Dec. 1998, *E. Barbosa et al. 240* (MBM); Parque Estadual do Pico Marumbi, 17 July 2000, *S. Dala Rosa 106* (UPCB); Piraquara, Serra do Mar, along a trail on W slope of Morro do Canal, 15 Oct. 2005, *P.W. Fritsch et al. 1807* (CAS, MBM, UEC); Rio Taquari, 29 Sep. 1951, *G. Hatschbach s.n.* (MBM 23454); Morro do Canal, 9 Jan. 2004, *O.S. Ribas et al. 5760* (MBM); Morro do Canal, *O.S. Ribas et al. 5848* (MBM, SPF); Morro do Canal, 18 Sep. 2004, *E.J. Stange 6* (UPCB); Quatro Barras, Rio Taquari, 8 Oct. 1968, *G. Hatschbach 19951* (HB, K, MBM, UPCB); Rio Taquari, 20 Oct. 1971, *G. Hatschbach 27669* (MBM); Rio Taquari, 21 Jan. 1975, *G. Hatschbach 35784* (MBM); Morro Anhangava, 23 Sep. 1992, *C.V. Roderjan 1018* (MBM). **Rio de Janeiro:** Itatiaia, Retiro, 18 Oct. 1903, *P.K.H. Dusen 29* (S); Retiro, 18 Oct. 1903, *P.K.H. Dusen 301* (R); 20 Oct. 1903, *P.K.H. Dusen 2023* (S); Santa Maria Madalena, Alto do Desengano, Oct. 1934, *J. Lima dos Santos* 277 (B, RB); Parque Estadual do Desengano, Pedra do Desengano, 26 Mar. 2002, *A.Q. Lobão et al. 667* (SPF); Parque Estadual do Desengano, Pedra do Desengano, 5 Oct. 1984, *G. Martinelli et al. 13155* (UPCB). **Santa Catarina:** Campo Alegre, Serra do Iquererim, 18 Oct. 1957, *R. Reitz & R.M. Klein 5249* (B, NY); Morro do Iquererim, 10 Jan. 1958, *R. Reitz & R.M. Klein 6132* (UPCB).

4. Symplocos falcata Brand in Engl., Pflanzenr. IV. 242 (6):71. 1901. TYPE.— BRAZIL. Rio de Janeiro: Serra do Alto do Macahé, 1889, *A.F.M. Glaziou 17473* (holotype: B destroyed; lectotype, here designated: G!; isolectotypes, C, K!, P, photo of C in NY!).

Symplocos aegrota Brand in Engl., Pflanzenr. IV. 242 (6):71. 1901. TYPE.— BRAZIL. Rio de Janeiro: "Bei Nova Friburgo" (protologue), 1885, *A.F.M. Glaziou 15203* (holotype: B destroyed; photo of holotype: NY!, RFA!; lectotype, here designated: G!; isolectotypes: K!, P).

Symplocos ascendens Brand in Engl., Pflanzenr. IV. 242 (6):71. 1901. TYPE.— BRAZIL. Rio de Janeiro: "Alto do Macahé bei Nova Friburgo" (protologue), 1892, *A.F.M. Glaziou 20212* (holotype: B destroyed; lectotype, here designated: K!; isolectotypes: C, G!, P, US, photo of C in NY!, RFA!, photo of US in RFA!).

Symplocos densiflora Brand in Engl., Pflanzenr. IV. 242 (6):71. 1901. TYPE.— BRAZIL. Minas Gerais: "Rancho do Morro Cavado" (protologue), 1876, *A.F.M. Glaziou 7769* (holotype: B destroyed; lectotype, here designated: G!; isolectotypes: K!, P).

Symplocos densiflora Brand var. *minor* Brand in Engl., Pflanzenr. IV. 242 (6):71. 1901. TYPE.— BRAZIL. São Paulo: "Campos da Bocaina" (protologue), 1878, *A.F.M. Glaziou 11167* (holotype: B destroyed; lectotype, here designated: K!; isolectotype: P).

We selected the material from G as lectotype of *S. falcata* because it includes a date and the locality cited on the protologue. *Symplocos aegrota* was based on three syntypes: *Glaziou 15203*, *17129*, and *17696*. We chose to lectotypify this name on *Glaziou 15203* because all the specimens within this collection match the protologue and it is fairly well represented in herbaria. We specifically designated the specimen from G as lectotype because of its label information, which matches the protologue. The holotype of *S. ascendens* was destroyed during World War II. We chose the specimen from K as lectotype because its label is more complete when compared with the type from G. *Symplocos densiflora* var. *densiflora* is based on two syntypes: *Glaziou 6695* and *7769*. We selected *Glaziou 7769* from G as lectotype because it has the exact location mentioned by Brand (1901) on its label. The holotype of *S. densiflora* var. *minor* (*Glaziou 11167*) was also destroyed in World War II. We excluded *Glaziou 11167* from G from the type collection because its locality does not agree with the protologue. We designated the material from K as lectotype because it is the only material of the type collection seen with label information that agrees with the protologue.

Tree or rarely shrub 2–25 m tall. Branches flattened to ± terete, striate, fissured or smooth, white-, golden yellow-, or ferrugineous-sericeous-tomentose, -strigose, or occasionally -hirsute, glabrescent. Petiole 2–20 mm long, adaxially flat or slightly concave, white-, golden yellow-, or ferrugineous-sericeous-tomentose or -strigose, glabrescent; leaf blade elliptic, oblong, or obovate, 5–16 × 1.8–4 cm, abaxially and adaxially densely white-, golden yellow-, or ferrugineous-sericeous-tomentose or -strigose, usually glabrescent abaxially and adaxially, secondary and tertiary veins highly branched near midvein and margin, base attenuate or occasionally cuneate to nearly rounded, margin conspicuously serrate on distal ¾, less often serrulate or rarely entire, marginal and apical glands usually early caducous, persistent glands 0 to 8 per cm, apex commonly acuminate or occasionally nearly acute, acumen (when present) 2–35 mm long. Inflorescence 4–8 mm long, 1- to 10-flowered; bracts 6 to numerous, abaxially densely white-, golden yellow-, or ferrugineous-sericeous-tomentose or -strigillose, margin frequently ciliate; the two basal bracts usually early caducous, deltoid to rotund, keeled, 2–3 × 0.8–1.2 mm, apex acute to rounded, apical gland usually lacking; other bracts 1–5 × 0.5–2.5 mm, apices of basalmost obtuse or rounded proximally, gradually more acute distally. Flower 3–4.5 mm long; hypanthium 0.8–1.2 mm long, glabrous; calyx lobes deltoid or occasionally rotund, 1–1.5 × 1–1.5 mm, densely white-, golden yellow-, or ferrugineous-sericeous-tomentose or -strigillose abaxially; corolla lobes 5(6), ascending or spreading, white, cream, or green, broadly elliptic to rotund, 2–3.5 × 1–2 mm, densely white-, golden yellow-, or ferrugineous-sericeous-tomentose or -strigillose abaxially, rarely only medially or glabrous. Stamens 25 to 35, exceeding and partly or totally obscuring gynoecium; filaments 0.5–2 mm long; anthers white or greenish white. Disc 0.8–1.3 mm in diameter, flat, slightly rugose, glabrous or rarely sparsely pubescent; style 0.5–1 mm long, glabrous. Fruit 2(3)-locular, cylindrical or nearly so, 8–10 × 4–6 mm, disc not enlarged and not distended beyond persistent calyx; calyx lobes erect to tightly appressed to disc, white-, golden yellow-, or ferrugineous-sericeous-tomentose or -strigillose, rarely glabrescent. Seed 1, 5–6 × 0.8–1.5 mm.

VERNACULAR NAMES.— canela (*M. Kuhlmann 2048* (MBM)), congonha (*P. Campos Porto 831* (R, RB)), congonha da mata (Bidá 1995).

ILLUSTRATION.— Figure 8.

PHOTOGRAPHIC IMAGES.— Figure 1D, 11.

PHENOLOGY.— Flowering usually from September to December, occasionally in February or

June to August; fruiting usually from November to February, occasionally in March or April or June to October.

Distribution and habitat.— *Symplocos falcata* is one of the most common and widespread species of section *Neosymplocos* in southeastern Brazil (São Paulo, Minas Gerais, Rio de Janeiro, and Espírito Santo, near the border with Minas Gerais). This species occurs mainly in low and high montane ombrophilous forest of the Serra do Mar (200 to 1900 m elevation) as understory (partial shade) or mid-canopy trees. In elfin forest it can be a shrub or small tree (1100 to 2400 m elevation). It also can be found in riparian situations, araucaria forest, "brejo" (marshes partially and permanently inundated by water), disturbed forest formations, and secondary vegetation. Distribution map, Figure 7.

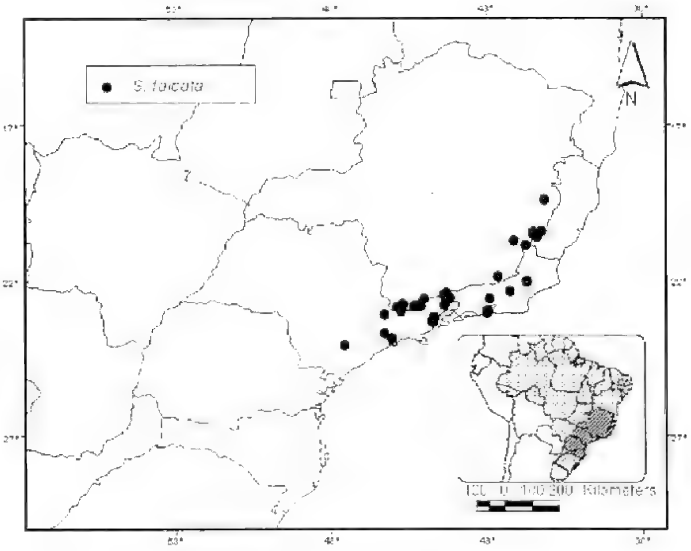

Figure 7. Distribution of *Symplocos falcata*.

Discussion.— *Symplocos falcata* is readily distinguished by the combination of its pubescent young leaves, densely sericeous-tomentose or strigillose calyx lobes at least when young, ascending or spreading corolla lobes, white to greenish white anthers, and fruit 8–10 mm long. In leaf size and shape *S. falcata* is most similar to *S. altissima* and *S. nitidiflora*. The leaves of *S. altissima*, however, are glabrous, and *S. nitidiflora* has strongly reflexed corolla lobes and yellow anthers. In addition, *S. nitidiflora* has larger pollen, with mesocolpia possessing a thick layer of sexine and a thinner layer of nexine-1, whereas that of *S. falcata* is smaller, with mesocolpia possessing a thinner layer of sexine and a thicker layer of nexine-1 (Occhioni 1975a). In leaf shape, size, and margin, and anther color, *S. falcata* is similar to *S. corymboclados*. The latter, however, has smaller fruit (5–7 mm long) with glabrous calyx lobes.

Symplocos falcata exhibits significant morphological variation correlated with habitat and elevation, and this variation is reflected in the several names published that here are relegated to synonymy. The component of *S. falcata* largely encompassed by *S. aegrota, sensu* Brand (1901), occurs in windy and humid areas of elfin forest. The most important characters used by Brand (1901) to distinguish *S. aegrota* from *S. falcata* were an acute leaf apex and an entire leaf margin (versus acuminate and serrate to serrulate). Several specimens collected in low and high montane ombrophilous forest in Rio de Janeiro, however, show considerable overlap in these characters. The characters that separate *S. densiflora* from *S. falcata* are hirsute (versus tomentose-sericeous) branches and obovate (versus elliptic) leaves that are abaxially strigose (versus sericeous-tomentose). Our field observations at Itatiaia and Camanducaia, however, revealed that individuals occurring in the understory (as shrubs or small trees) have characteristics of *S. densiflora* and the upper branches of mid-canopy trees have those of *S. falcata*. Frequently, the lower branches (in partial shade) of the mid-canopy trees have hirsute branches and obovate leaves that are abaxially strigose. Furthermore, several collections (*Glaziou 5888*, *Dusen 14240*, and *Mgf. & App. 10403*) from Rio

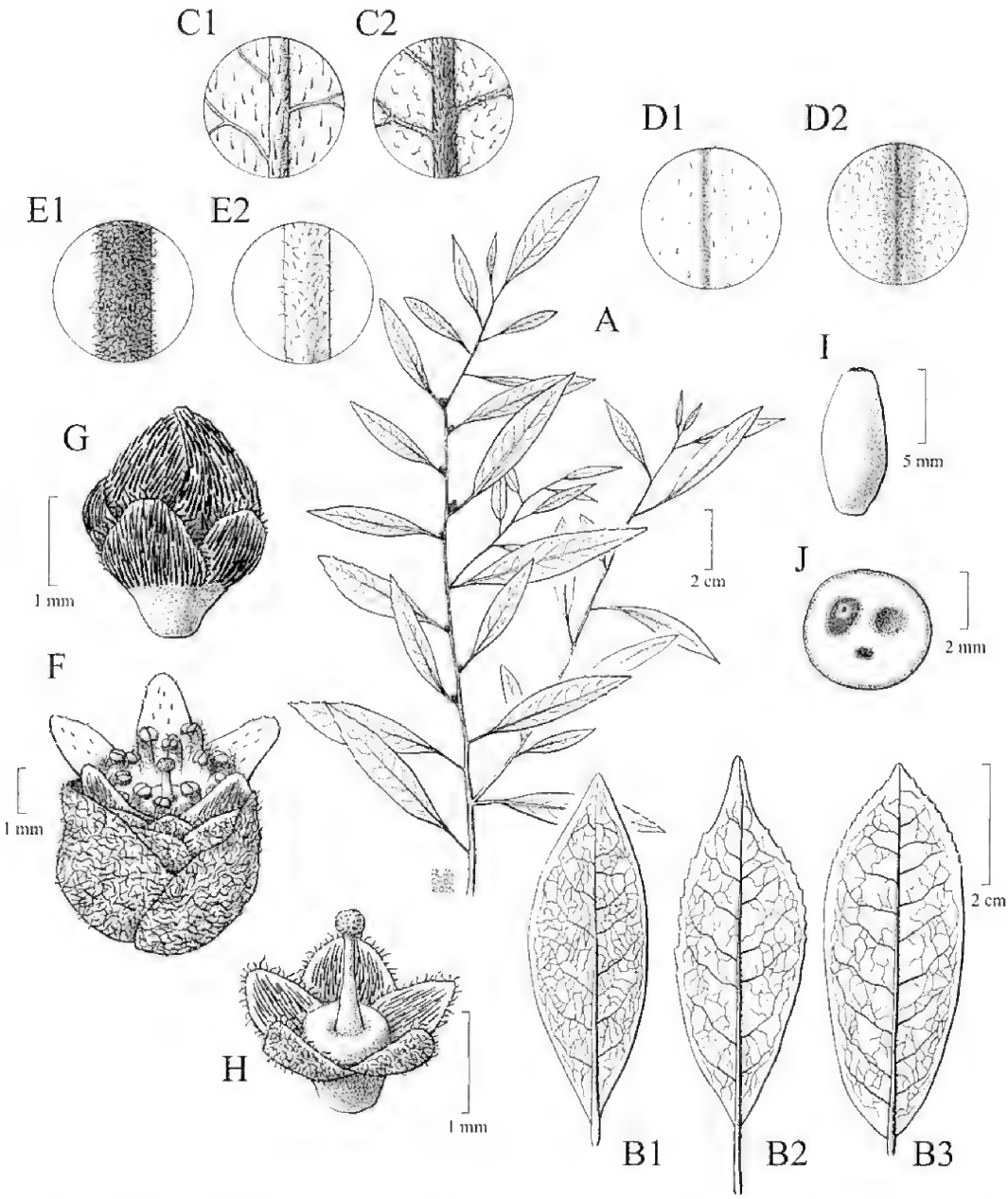

FIGURE 8. *Symplocos falcata* Brand. A. Flowering branch; B1, B2, and B3. Variation in leaf morphology (abaxial surface); C1 and C2. Variation in leaf indument (abaxial surface); D1 and D2. Variation in leaf indument (adaxial surface); E1 and E2. Variation in branch indument; F. Flower at anthesis with subtending bracts and androecium opened outward to show ovary apex, style, and stigma; G. Floral bud; H. Flower with corolla and androecium removed; I. Mature fruit; J. Mature fruit in cross-section. (A, B2, C2, D1, and E2–H from *Glaziou 17473*; B1, D2, and E1 from *Glaziou 15203*; B3 and C1 from *Glaziou 7769*; I–J from *Glaziou 17129*).

de Janeiro show these purported species differences on the same specimen. In circumscribing *S. ascendens*, Brand (1901) used only the ascending petioles to separate it from *S. falcata*. This, however, appears to be an artifact of the drying process, and even *S. falcata, sensu* Brand (1901), has such petioles. Brand (1901) distinguishes *S. densiflora* vars. *densiflora* and *minor* by leaves 8–12 versus 7–9 cm long, respectively. This difference is not sufficient for the recognition of varieties because it is a single character uncorrelated with geography.

ADDITIONAL SPECIMENS EXAMINED.— **Brazil. Espírito Santo:** Dores do Rio Preto, Parque Nacional do Caparaó, near Casa Queimada, 19 Oct. 1999, *F.F. Mazine et al. 202* (ESA); Iúna, Parque Nacional do Caparaó, between Arrozal and Rancho dos Cabritos, 18 Feb. 2000, *V.C. Souza et al. 23397* (ESA). **Minas Gerais:** Camanducaia, Monte Verde District, Serra da Mantiqueira, 8 km from Monte Verde, on the trail to Pedra Partida and Pedra Redonda, *F. Almeda et al. 8782* (CAS, UEC); Monte Verde District, Serra da Mantiqueira, 9 Nov. 2004, *F. Almeda et al. 8788* (CAS, UEC); Monte Verde District, Serra da Mantiqueira, 9 Nov. 2004, *F. Almeda et al. 8790* (CAS, UEC); Monte Verde District, 29 Sep. 2004, *J.L.M. Aranha Filho et al. 29* (UEC); Monte Verde District, 30 Sep. 2006, *J.L.M. Aranha Filho et al. 43* (UEC); Mata do Altair, near the road, 8 Dec. 2000, *G.S. França 211* (BHCB, HRCB); Mata do Altair, near the road, 12 Oct. 2000, *G.S. França & J.R. Stehmann 125* (BHCB, HRCB); near Monte Verde District, 19 Nov. 1979, *H. de F. Leitão Filho & R.R. Rodrigues 10670* (UEC); Gonçalves Road, 23 Oct. 2001, *J.R. Stehmann & I.B. Castro 3001* (BHCB, HRCB); Caparaó, Serra do Caparaó, 13 Sep. 1941, *A.C. Brade 16932* (MBM, RB, UPCB (2)); Parque Nacional do Caparaó, trail to Pico da Bandeira, 15 June 1991, *G. Hatschbach & J.M. Silva 55522* (MBM, SPF); Serra do Brigadeiro, 12 Jan. 1995, *L.S. Leoni 2759* (UPCB); Parque Nacional, 29 Sep. 1993, *L.S. Leoni et al. 3076* (HB, UPCB); Parque Nacional do Caparaó, trail to Tronqueira-Terrerão, near the river, 29 Sep. 1995, *J.A. Lombardi 939* (BHCB, HRCB); Pico do Luiz Inácio, 21 Oct. 1947, *A.X. Moreira 46* (R); Parque Nacional do Caparaó, trail to Pico da Bandeira, 12 Dec. 1998, *J. Paula-Souza et al. 2109* (ESA); Parque Nacional do Caparaó, trail between Tronqueira and Pico da Bandeira, 2 Sep. 1996, *V.C. Souza et al. 12147* (ESA, SPF); Delfim Moreira, between Delfim Moreira and Itajubá, 17 Mar. 1939, *A. Gehrt & M. Kuhlmann s.n.* (SP 40077); Paraíso, between Pedra São Domingos and Pessegueiro, 14 Oct. 2000, *G.S. França & J.R. Stehmann 158* (BHCB, HRCB). **Rio de Janeiro:** Itatiaia, Sep. 1934, *A.C. Brade 14050* (RB); 1918, *P. Campos Porto 831* (R, RB); 18 Oct. 1903, *P.K.H. Dusen s.n.* (K 1978111, S); 18 June 1902, *P.K.H. Dusen 573* (R (2); S, SP); 20 Oct. 1903, *P.K.H. Dusen 2135* (S); 24 June 1873, *A.F.M. Glaziou 6695* (K, NY); Caminho das Macieiras, 18 Oct.1922, *J.G. Kuhlmann s.n.* (R 111294, RB 22314); road Registro × Planalto, Km 9, 16 Sep. 1974, *P. Occhioni 6240* (RFA); road to Planalto, Km 5, 16 Sep. 1974, *P. Occhioni 6255* (RFA); Macieiras, 15 Mar. 1975, *P. Occhioni 7064* (RFA); road to Registro, Agulhas Negras, 12 Mar. 1975, *P. Occhioni 7100* (RFA); road Registro-Planalto, 11 Dec. 1975, *P. Occhioni 7830* (RFA); Registro, on the road to Planalto do Itatiaia, Km 2, 17 Jan. 1979, *P. Occhioni 8702* (MBM, RFA); 10 Jan. 1896, *E.H.G. Ule 644* (R); Nova Iguaçu, Tinguá REBIO, Pico do Tinguá, Rala Trail, Sapé, 30 Jan. 2002, *H.C. de Lima et al. 5988* (RB); Tinguá REBIO, Pico do Tinguá, Rala Trail, Sapé, 30 Jan. 2002, *H.C. de Lima et al. 6019* (RB); Petrópolis, 1889, *A.F.M. Glaziou 17696* (G, K); Rio de Janeiro, Serra da Tijuca, 6 Feb. 1946, *Altamiro et al. 51* (MBM, RB, UPCB); Serra da Tijuca, 6 Mar. 1946, *A.A. Edmund. & Walter 51* (R, UPCB); Paula e Virgínia, Tijuca, Oct. 1964, *A.P. Duarte 8668* (GUA, HB, RB, UPCB (2)); Tijuca, Pedra do Conde, 25 Sep. 1928, *A. Ducke s.n.* (RB 22312); Pico da Tijuca, 30 Sep. 1900, *E. Hemmendorff 3241* (S); Archer, Tijuca, Sep. 1915, *F.C. Hoehne 311* (SP); Pedra do Cônego, Tijuca, 16 Oct. 1928, *J.G. Kuhlmann s.n.* (RB 148776); Santa Maria Madalena, Pedra Dubois, 25 June 1987, *C. Farney et al. 1439* (RB); Pedra Dubois, 22 Feb. 1983, *T. Plowman & H. C. de Lima 12863* (NY); Teresópolis, Parque Nacional da Serra dos Órgãos, near the upper part of the Rancho Frio Trail, 9 Mar. 2005, *C. Seele 1055* (RB); Parque Nacional da Serra dos Órgãos, trail to Rancho Frio, 11 Mar. 2005, *J. Wesenberg & R. Engelmann 628* (RB); no location indicated, 1883-1884, *A.F.M. Glaziou s.n.* (NY 486948); *A.F.M. Glaziou 5888* (S); *A.F.M. Glaziou 17636* (G). **São Paulo:** Bocaina, Lageado, 7 Dec. 1952, *Mgf. & App. 10403* (GUA, RB, UPCB); Lageado, Dec. 1972, *J. Reis s.n.* (RFA 15715); Serra da Bocaina, road to São José do Barreiro-Silveiras, Km 16, 2 Jan. 1981, *G.J. Shepherd & S.L.K. Shepherd 12859* (UEC); Campos do Jordão, Pico do Itapeva, 6 Nov. 1987, *S.M. Carmello-Guerreiro et al. 13* (SPF); Parque Estadual, 16 Oct. 1984, *J.P.M. Carvalho & M. de J. Robin s.n.* (MBM 235530); 26 Sep. 1980, *J.E.R. Collares 48* (RB); 27 Sep. 1980, *J.E.R. Collares 64* (RB); road between Reserva do Instituto Florestal and São José dos Alpes, ca. 6 km, 29 Sep. 1984, *L.S. Kinoshita et*

al. 16544 (UEC, UPCB); Umuarama, 28 Jan. 1935, *M. Kuhlmann s.n.* (SP 32527, UPCB 26734); Umuarama, 22 Nov. 1949, *M. Kuhlmann 2048* (SP, SPF, UPCB); Campo das Macieiras, 13 June 1950, *M. Kuhlmann 2531* (SP, UPCB); Guarda Farm, Horto Florestal, 15 Dec. 1966, *J. Mattos & N. Mattos 14362* (ESA, SP, UPCB); Fazenda da Guarda, Horto Florestal, 17 Dec. 1966, *J. Mattos & N. Mattos 14469* (SP); 16 Feb. 1981, *Messias 48* (RB); road to Pico Itapeva, 12 Jan. 1977, *P. Occhioni 8009* (MBM, RFA); road to Pico Itapeva, 12 Jan. 1977, *P. Occhioni 8024* (RFA); Parque Estadual, trail to Rio Sapucaí, 10 Oct. 2001, *J.R. Pirani et al. 4896* (MBM, NY, SP, SPF); Parque Estadual, Pinheiro Seco, 16 Oct. 1984, *M. de J. Robin & J.P.M. Carvalho s.n.* (MBM 235531); Parque Estadual de Campos do Jordão, Instituto Florestal, São José dos Alpes, 22 Feb. 1984, *M. de J. Robin & J.P.M. Carvalho 8398* (UPCB); Parque Estadual de Campos de Jordão, Instituto Florestal, trail to the waterfall, 7 Jan. 1985, *M. de J. Robin & A.D. Pereira 212* (MBM, UPCB); 21 Nov. 1980, *A.A.B. Rubens 198* (RB); Parque Estadual, 27 Apr. 1981, *A.A.B. Rubens 255* (RB); 24 June 1981, *A.A.B. Rubens 264* (RB); Parque Estadual de Campos de Jordão, 17 Aug. 1980, *J.C.C. Ururahy 21* (RB); Cunha, margin of Rio Paraibuna, 28 Jan. 2004, *F.A.R.D.P. Arzolla 425* (UEC); Parque Estadual da Serra do Mar, 30 Mar. 1994; *J.B. Baitello 594* (UPCB); Parque Estadual da Serra do Mar, Núcleo Cunha, 13 Dec. 1996, *D.F. Bertani et al. 1* (ESA, SPF, UEC); Estação Experimental da Serra do Mar, Núcleo Cunha, Morro da Marlene, trail to elfin forest, *A.R. Ferretti 140* (ESA, HRCB, SP, SPF, UEC); Parque Estadual da Serra do Mar, Núcleo Cunha-Indaiá, Rio Bonito Trail, 28 Jan. 2004, *N.M. Ivanauskas et al. 5069* (ESA); Parque Estadual da Serra do Mar, Rio Bonito, 17 Aug. 1994, *M.L. Kawasaki & G.A.D.C. Franco 571* (HRCB, SPF, UEC); Parque Estadual da Serra do Mar, Pedreira, 18 Aug. 1994, *M.L. Kawasaki & G.A.D.C. Franco 1252* (HRCB, SPF, UEC, UPCB); Santo André, Alto da Serra, 3 Oct. 1912, *P.K.H. Dusen 14240* (NY, S); Alto da Serra, Estação Biológica, 2 Oct. 1931, *F.C. Hoehne s.n.* (SP 28310); Reserva Biológica do Alto da Serra de Paranapiacaba, 6 Nov. 1991, *M. Kirizawa et al. 2568* (SP); Estação Biológica, 30 Sep. 1922, *J.G. Kuhlmann s.n.* (RB 162879); São Caetano do Sul, 7 Oct. 1922, *J.G. Kuhlmann s.n.* (RB 21948); São José do Barreiro, Serra da Bocaina, 29 June 1994, *K.D. Barreto 2696* (ESA); 21 Sep. 1997, *L. Freitas 299* (UEC).

5. Symplocos glandulosomarginata Hoehne ["*S. glanduloso-marginata*"], Arq. Bot. São Paulo 1(1):37–38, tab. 44. 1938. TYPE.— BRAZIL. São Paulo: São Paulo, Jardim Botânico, 10 November 1932, *O. Handro s.n.* (holotype: SP!; isotypes: B!, K!, MBM!, NY (3)!, S!, US, photo of US in RFA!).

Shrub or tree 2–25 m tall. Branches ± terete, striate, fissured, white-, golden yellow-, or ferrugineous-tomentose, glabrescent. Petiole 2–5 mm long, adaxially flat, white-, golden yellow-, or ferrugineous-tomentose, glabrescent; leaf blade narrowly elliptic or occasionally oblanceolate or obovate, 3.5–5 × 0.5–1.5 cm, abaxially densely white-, golden yellow-, or ferrugineous-tomentose, glabrescent, adaxially rarely sparsely strigose on surface and occasionally puberulent on basal half of midvein, otherwise glabrous, glabrescent, secondary and tertiary veins sparsely branched near midvein and margin, base attenuate or nearly so, margin entire, marginal and apical glands persistent or rarely a few caducous, persistent glands 13 to 25 per cm, apex acute or occasionally obtuse-rounded, rarely hooked-retuse. Inflorescence 5–7 mm long, 1- to 7-flowered; bracts 6 to 22; the two basal bracts usually early caducous, deltoid, keeled, 0.8–1 × 0.5–0.7 mm, glabrous, margin not ciliate, apex acute or subacute, apical gland usually lacking; other bracts 1–1.5 × 1–1.5 mm, densely white-, golden yellow-, or ferrugineous-tomentose abaxially, margin ciliate, apices of basalmost obtuse or nearly rounded, gradually more rounded distally. Flower 3–4 mm long; hypanthium 0.8–1 mm long, glabrous; calyx lobes deltoid to rotund, 1–1.5 × 1–1.5 mm, glabrous; corolla lobes 5(6), broadly elliptic to obovate, 2–3 × 1–1.5 mm, white to greenish white, glabrous or rarely sparsely pubescent. Stamens 25 to 35, exceeding and obscuring gynoecium; filaments 0.5–2 mm long. Disc 1–1.5 mm in diameter, flat, slightly rugose, glabrous or rarely sparsely pubescent; style 0.5–0.8 mm long, glabrous. Fruit (1 or 2)3-locular, ellipsoid, 6–9 × 3–5 mm, disc enlarged and distended beyond persistent calyx; calyx lobes erect, glabrous. Seed 1, ca. 5 × 2 mm.

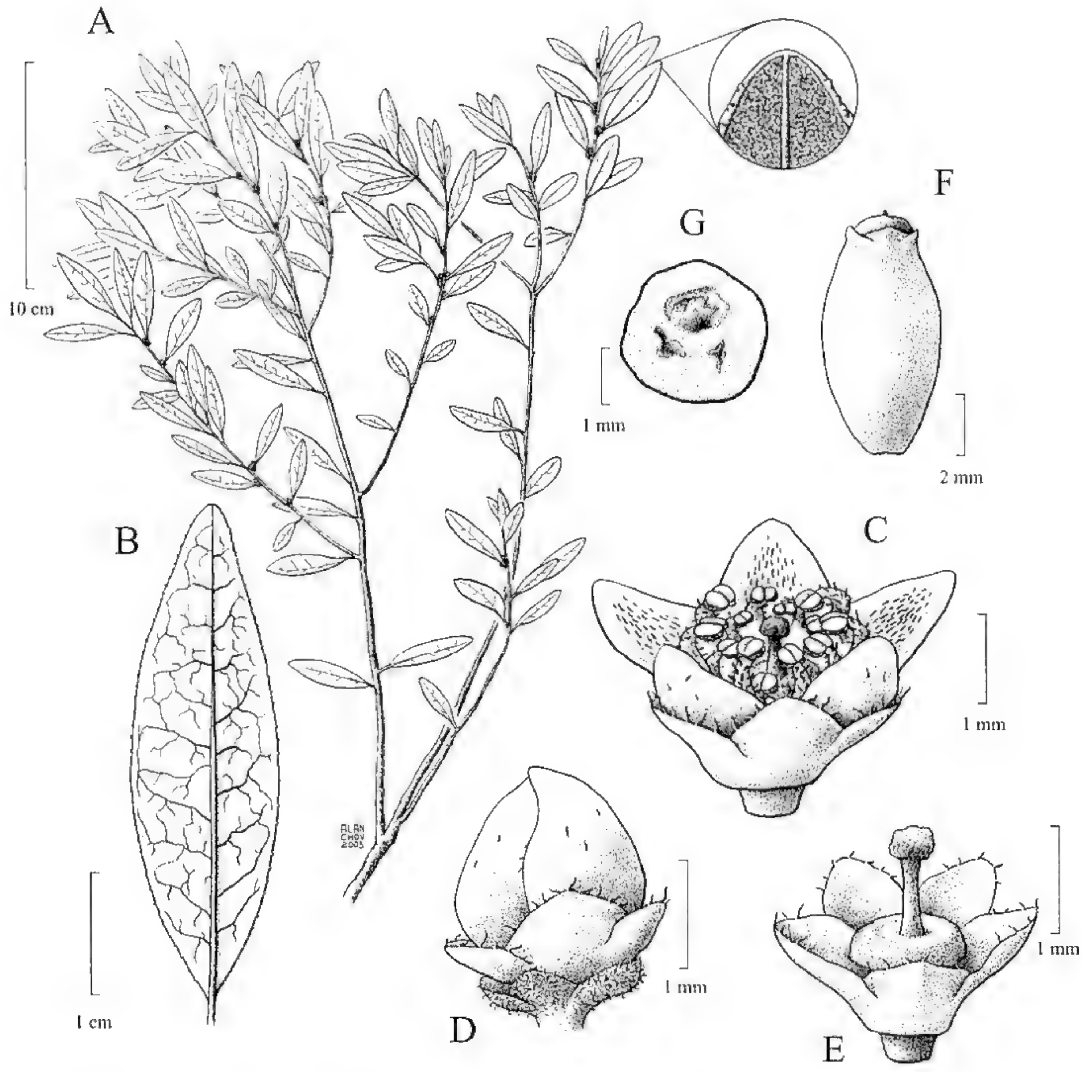

FIGURE 9. *Symplocos glandulosomarginata* Hoehne. A. Flowering branch with leaf indument detail; B. Representative leaf (abaxial surface); C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud and subtending bracts; E. Flower with corolla and androecium removed; F. Mature fruit; G. Mature fruit in cross-section. (A–E from *Handro s.n.*; F–G from *Hatschbach 39767*).

VERNACULAR NAMES.— falsa caneta (Bidá 1995), maria mole (*G. Tiepolo 13* (MBM)).

ILLUSTRATION.— Figure 9.

PHOTOGRAPHIC IMAGE.— Figure 1B.

PHENOLOGY.— Flowering from September to November; fruiting from December to February, occasionally May and July.

DISTRIBUTION AND HABITAT.— *Symplocos glandulosomarginata* occurs mainly in the Serra do Mar of Paraná, reaching northeastern Santa Catarina and northeastern São Paulo (450 to 1350 m elevation). This species can be found in the western regions of Paraná in riparian situations, brejo, and araucaria, montane ombrophilous, semideciduous, and secondary forests. *Symplocos glandulo-*

somarginata is usually a mid-canopy tree but also grows in transitional habitats between montane ombrophilous and elfin forest (1000 to 1500 m elevation). In the latter situation, it is a small tree or even a shrub. Distribution map, Figure 2.

Discussion.— *Symplocos glandulosomarginata* is easily recognized by its many persistent glands on the mature leaves (13 to 25 per cm). This species is also characterized by the combination of sparsely puberulent leaves on the basal half of the midvein adaxially, tomentose indument (when young) abaxially, and a fruit with an enlarged disc distended beyond the persistent calyx. The species resembles *S. tenuifolia* in the sapling stage, and *S. glaziovii* in leaf indument, size, and shape, but both of these species have few or no persistent glands on mature leaves (0 to 8 per cm).

Additional specimens examined.— **Brazil. Paraná:** Antonina, trail to Pico Caratuva, 19 Oct. 2005, *P.W. Fritsch et al. 1832* (CAS, MBM, UEC); Balsa Nova, Serra São Luís, 18 July 1971, *G. Hatschbach 26859* (MBM, UPCB); Bocaiúva do Sul, Serra de Santana, 30 Jan. 1996, *J.T. Motta et al. 3017* (BHCB, MBM, NY, SPF); Serra da Bocaina, 11 Nov. 1998, *J.M. Silva & L.M. Abe 2622* (BHCB, ESA, MBM, SP); Campina da Cascavel, 8 Nov. 1976, *G. Hatschbach 39177* (MBM, NY, UEC); Campo Grande, Nov. 1902, *G. Edwall s.n.* (SPF 83567); Guaraqueçaba, Serra Gigante, 21 Dec. 2002, *A.Y. Mocochinski 232* (MBM); Guaratuba, 23 Feb. 2002, *O.S. Ribas et al. 4421* (BHCB, ESA, MBM); Morretes, Parque Estadual do Pico Marumbi, 3 Nov. 1999, *S. Dala Rosa 56* (UPCB), Rio Arraial, 11 Nov. 1965, *G. Hatschbach 13112* (MBM (2), UPCB); Palmeira, Café Highway, Rio Tibagi, 22 Oct. 1965, *G. Hatschbach 13053* (HB, MBM (2), NY, UPCB); Santa Rita, 26 Oct. 1982, *G. Hatschbach 45713* (MBM); Piraquara, Carvalho, 13 Sep. 1911, *P.K.H. Dusen 12195* (S); road to and vicinity of SANEPAR Water Company, 500 m from Represa do Carvalhinho, 17 Oct. 2005, *P.W. Fritsch & J.L.M. Aranha Filho 1826* (CAS, MBM, UEC); Serra do Mar, along a trail on W slope of Morro do Canal, 15 Oct. 2005, *P.W. Fritsch et al. 1808* (CAS, MBM, UEC); Serra do Mar, along a trail on W slope of Morro do Canal, 15 Oct. 2005, *P.W. Fritsch et al. 1809* (CAS, UEC); Serra do Emboque, Vale das Trutas, 3 Feb. 1992, *G. Hatschbach 50102* (MBM); Represa de Piraquara, 8 Nov. 1984, *R. Kummrow 1730* (MBM, NY); Mananciais da Serra, 10 Nov. 1976, *Y.S. Kuniyoshi 4077* (HB); Mananciais da Serra, Morro do Canal, 19 Jan. 1999, *A. Lacerda 275* (MBM, UPCB); Mananciais da Serra, Jan. 2005, *M. Reginatto 177* (UPCB); Morro do Canal, 3 Feb. 2004, *O.S. Ribas et al. 5871* (MBM, SPF); Quatro Barras, Pico do Anhangava, 11 Feb. 1992, *M.V. Capranica s.n.* (UPCB 26175); Serra da Graciosa, Rio Corvo, 2 July 1995, *A.C. Cervi & C. Kozera 6101* (MBM, UEC, UPCB); Rio Corvo, 7 Nov. 1966, *G. Hatschbach 15089* (MBM (2), RFA, UPCB); Rio Graciosa, Rio Corvo, 19 Nov. 1998, *G. Hatschbach et al. 68818* (MBM, UPCB); Pico do Anhangava, 11 Feb. 1992, *T. Plowman s.n.* (NY 486774); Serra da Baitaca, 22 Oct. 1993, *G. Tiepolo 13* (MBM); Serra da Baitaca, 23 Dec. 1993, *G. Tiepolo 47* (MBM); Serra da Baitaca, 15 Jan. 1997, *G. Tiepolo et al. 564* (UPCB); São José dos Pinhais, Zinco, 21 Jan. 1999, *J. Cordeiro et al. 1512* (B, MBM, SPF); Governador Lupion Highway, Rio Pequeno, 5 Nov. 1961, *G. Hatschbach s.n.* (HB 16506, MBM 23461, UPCB 3413); Rio Pequeno, 5 Nov. 1966, *G. Hatschbach 22851* (MBM, NY, S, UPCB); Guaricana, 5 Nov. 1975, *G. Hatschbach 34895* (MBM, UEC); Guaricana, 17 Feb. 1977, *G. Hatschbach 39767* (HB, MBM, NY, UEC); Córrego Fundo, 26 Jan. 1983, *G. Hatschbach 46053* (MBM); Colony Santo Andrade, 21 May 1980, *G. Hatschbach 43002* (MBM); Colony Roseira, 23 Feb. 1968, *C. Koczicki 85* (MBM, RFA); Mananciais da Serra, 25 Sep. 1997, *J.H.P. de Macedo s.n.* (MBM 251000); Guaricana, 24 Oct. 1997, *J.M. Silva et al. 2120* (MBM); Tijucas do Sul, Serra Papanduva, 6 Nov. 1998, *E. Barbosa et al. 197* (MBM); Ypiranga, 4 Sep. 1911, *P.K.H. Dusen 12143* (K, NY, S (2)); no location indicated, Joinville-Curitiba Highway, Km 47, 25 Nov. 1972, *P. Occhioni 5342* (RFA). **Santa Catarina:** Blumenau, Morro Spitzkopf, 21 Oct. 1959, *R. Reitz & R.M. Klein 1130* (B); Morro Spitzkopf, 23 Oct. 1959, *R. Reitz & R.M. Klein 4130* (K, NY); Campo Alegre, Serra do Iquererim, 19 Nov. 1992, *J. Cordeiro & C.B. Poliquesi 921* (MBM, UEC); Morro do Iquererim, 8 Nov. 1956, *L.B. Smith & R.M. Klein 7392* (B, R, S); Ibirama, Horto Florestal, 12 Nov. 1956, *L.B. Smith & R.M. Klein 7557* (NY, R, RB). **São Paulo:** Cunha, Parque Estadual da Serra do Mar, Núcleo Cunha-Indaiá, 28 Jan. 2004, *N.M. Ivanauskas et al. 5068* (ESA); Jundiaí, Reserva Biológica Municipal da Serra do Japi, 2 June 1998, *E.C. Leite 562* (UEC); no location indicated, road to Campo Grande, Nov. 1902, collector's name illegible *5792* (SP).

6. Symplocos glaziovii Brand in Engl., Pflanzenr. IV. 242 (6):73. 1901. **Type.**— **Brazil.** Rio de Janeiro: Alto do Macahé, 3 November 1881, *A.F.M. Glaziou 13469* (holotype: B destroyed; lec-

totype, here designated: NY 297019!; isolectotypes: BM!, C, G!, IAC!, IAN, K!, NY 297020!, P, photo of C in RFA!).

Several isotypes of *S. glaziovii* have been found during our revision. We selected one of the isotypes from NY (297019) as the lectotype because its label has the same date and locality as that in the protologue. Moreover, it has good flowering material.

Reportedly a small tree. Branches ± terete, striate, fissured, white-, golden yellow-, or ferrugineous-tomentose, glabrescent. Petiole 3–5 mm long, adaxially flat, white-, golden yellow-, or ferrugineous-tomentose, glabrescent; leaf blade oblanceolate or spatulate, 2–4 × 0.6–1.5 cm, abaxially densely white-, golden yellow-, or ferrugineous-tomentose, rarely glabrescent, adaxially sparsely puberulent on basal half of midvein and otherwise glabrous, secondary and tertiary veins sparsely branched near midvein and margin, glabrescent, base attenuate or nearly so, margin entire, marginal and apical glands usually caducous, persistent glands 0 to 8 per cm, apex hooked-retuse or occasionally obtuse, rarely acute. Inflorescence 3–8 mm long, 1- to 10-flowered; bracts 6 to numerous, white-, golden yellow-, or ferrugineous-tomentose abaxially; the two basal bracts usually early caducous, deltoid, keeled, 0.8–1.2 × 0.5–1.5 mm, margin not ciliate, apex acute or nearly so, apical gland usually lacking; other bracts 0.8–1.5 × 0.5–0.8 mm, margin ciliate, apices of basalmost rounded proximally, gradually more obtuse distally. Flower 1.5–3.5 mm long; hypanthium 0.8–1.1 mm long, glabrous; calyx lobes ± deltoid to rotund, 1–1.2 × 0.8–1.2 mm, sparsely white-, golden yellow-, or ferrugineous-tomentose mainly abaxial-medially, glabrescent; corolla lobes 5(6), reportedly pink, broadly elliptic to obovate, 1.7–2.3 × 0.8–1.2 mm, glabrous or sparsely pubescent. Stamens 25 to 30, exceeding and obscuring gynoecium; filaments 0.5–1.5 mm long. Disc 0.7–1.2 mm in diameter, flat, rugose, glabrous; style 0.4–0.6 mm long, glabrous. Fruit unknown.

VERNACULAR NAME.— None.

ILLUSTRATION.— Figure 10.

PHENOLOGY.— Flowering in November.

DISTRIBUTION AND HABITAT.— Like *Symplocos altissima*, *S. glaziovii* is reportedly endemic to Nova Friburgo (Rio de Janeiro) in elfin forest at ca. 2000 m elevation in the Serra dos Órgãos. Distribution map, Figure 2.

DISCUSSION.— The combination of leaves 2–4 × 0.6–1.5 cm that are tomentose abaxially (rarely glabrescent), margin with 0 to 8 per cm, style 0.4 to 0.6 mm long, and the disc flat distinguishes *Symplocos glaziovii* from all other species of *Neosymplocos*. The leaf morphology (size, shape, and indument) of *S. glaziovii* suggests that it is related to *S. glandulosomarginata*. The latter can be distinguished from *S. glaziovii* by its persistent glands along the margin (13 to 25 per cm).

7. Symplocos insolita Aranha, P.W. Fritsch, and Almeda, nom. nov. Replaced name: *Symplocos candelabra* Aranha, P.W. Fritsch, and Almeda, Proc. Calif. Acad. Sci. 56:296–299. 2005, non *S. candelabrum* Brand in Engl., Pflanzenr. IV. 242 (6):39. 1901. TYPE.— BRAZIL. Minas Gerais: Serra do Cipó, Santana do Riacho, 6 km S of the turnoff to Morro do Pilar on the road to Conceição do Mato Dentro, 1350 m, 19°15'40.7″S, 43°31'59.0″W, 22 November 2004, *F. Almeda, P.W. Fritsch, J.L.M. Aranha Filho & R. Belinello 8910* (holotype: UEC!; photo of holotype: MBM!; isotype: CAS!).

Brand (1901) described *Symplocos candelabrum* (section *Bobua* (DC.) Brand, subgenus *Hopea*) based on one collection from Australia (*Maiden s.n.*). Aranha Filho et al. (2005) described *S. candelabra* (from Brazil) based on *Almeda et al. 8910*. Both epithets are extremely similar, and therefore likely to be confused [Article 53.3 in the International Code of Botanical Nomenclature (McNeill et al. 2006)]. We here provide a replacement name for *S. candelabra*.

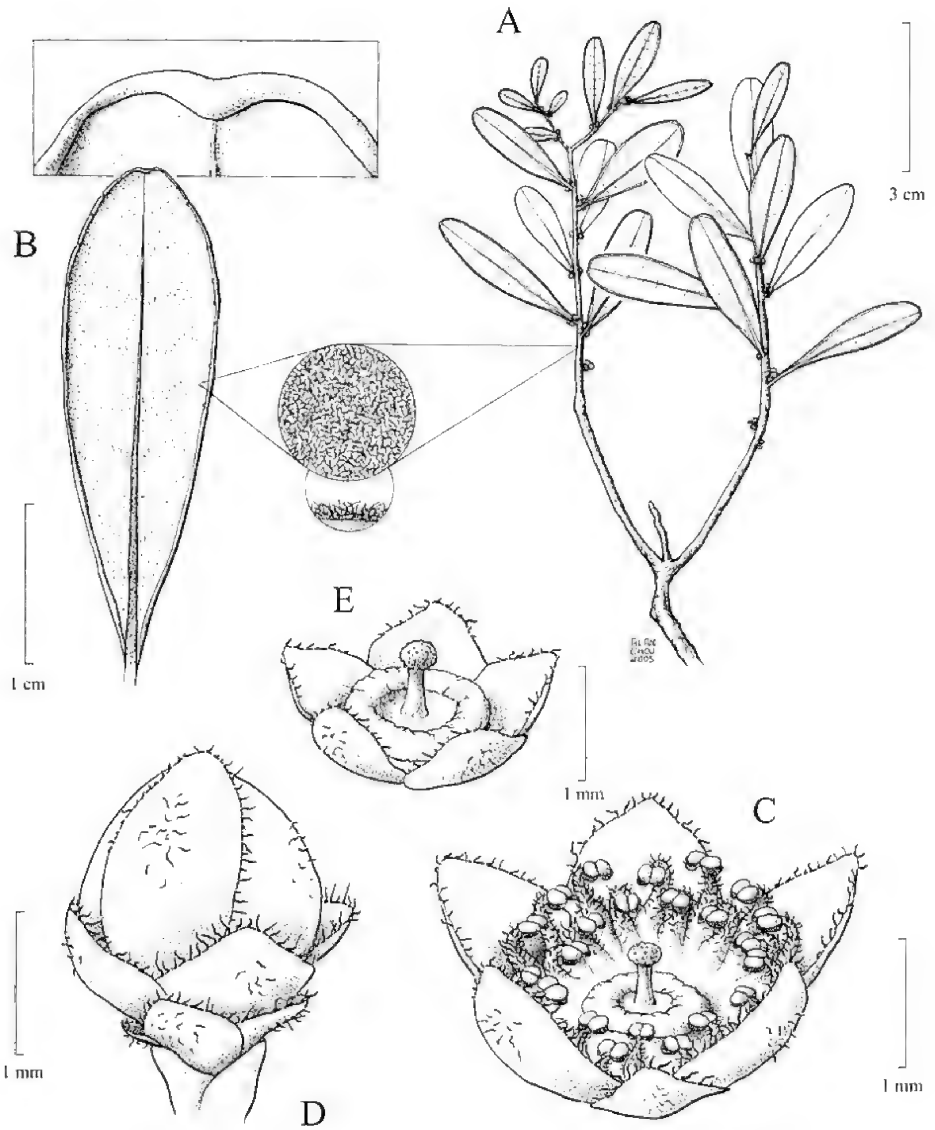

FIGURE 10. *Symplocos glaziovii* Brand. A. Flowering branch with branch indument detail; B. Representative leaf (abaxial surface), leaf indument detail, and close-up of leaf apex; C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud and subtending bracts; E. Flower with corolla and androecium removed. (A–E from *Glaziou 13469*).

Openly branched rigid candelabriform shrub ca. 1 m tall. Branches terete, striate, fissured, densely ferrugineous-hirsute, glabrescent. Petiole 1–3 mm long, adaxially flat, white- to ferrugineous-strigose, glabrescent; leaf blade rotund or subrotund, 1.1–5 × 0.9–3.5 cm, abaxially densely white- to ferrugineous-strigose, glabrescent, adaxially sparsely puberulent on basal half of midvein, otherwise glabrous, glabrescent, secondary and tertiary veins highly branched near midvein and margin, base cordate or subcordate, margin entire or occasionally inconspicuously serrulate mainly on distal half, apex obtuse-truncate marginal and apical glands usually early caducous, persistent glands 0 to 8 per cm. Inflorescence 6–10 mm long, 1- to 5- flowered; bracts 6 to 20; the two basal

bracts usually persistent, nearly deltoid to rotund, keeled, 1–2 × 0.75–1 mm, sparsely ferrugineous-strigillose mainly abaxial-medially, margin not ciliate, apex acute, obtuse to rounded, apical gland usually lacking; other bracts 0.5–1.5 × 1.5–4 mm, sparsely to densely ferrugineous-strigillose abaxially, apices of basalmost rounded, gradually more acute distally. Flower 5–8.5 mm long; hypanthium 1–1.5 mm long, glabrous; calyx lobes deltoid to occasionally subrotund, 1.5–2 × 1–2 mm, glabrous or sparsely pubescent, then glabrescent; corolla lobes 5(6 or 7), ascending, white, obovate to subrotund, 3–5 × 1.5–3 mm, glabrous or rarely sparsely pubescent. Stamens 25 to 35, exceeding and obscuring gynoecium; filaments 0.5–5 mm long; anthers yellow. Disc 1–1.2 mm in diameter, prominently elevated (0.7–1 mm), rugose, glabrous; style 0.5–0.7 mm long, glabrous. Fruit (2)3-locular, ovoid or ellipsoid, 7–9 × 3–5 mm, disc not enlarged and not distended beyond persistent calyx; calyx lobes tightly appressed to disc, glabrous. Seed 1, 4–5 × 1.5–2.5 mm.

Vernacular name.— None.

Illustration.— Figure 11.

Photographic image.— Aranha Filho et al. 2005.

Phenology.— Flowering in November; fruiting in February.

Distribution and habitat.— *Symplocos insolita* is known to us only from a single locality in the Serra do Cipó (old Km 132) at 1350 m elevation growing in an open and windy rocky site in campo rupestre. After extensive searching, we found only four plants of this species near what is probably the area where past collections were made. One collection has been made outside this area at the margin of a gallery forest among rocks. Distribution map, Figure 2.

Discussion.— *Symplocos insolita* is readily distinguished by its candelabriform habit (rare among *Symplocos* species), and the combination of a strigose leaf blade (when young) abaxially with the base cordate or subcordate, and prominently elevated (0.7 to 1 mm) disc. The only other species with a prominently elevated disc is *S. angulata*, which can be distinguished from *S. insolita* by the characters in the key.

Additional specimens examined.— **Brazil. Minas Gerais:** Conceição do Mato Dentro, Parque Natural Municipal do Ribeirão do Campo, 8 Nov. 2002, *R.C. Mota & P.L. Viana 1898* (BHCB, SPF); Jaboticatubas, Lagoa Santa-Conceição do Mato Dentro-Diamantina Highway, 4 Nov. 1972, *A.B. Joly CFSC 3687* (SP); Santana do Riacho, Belo Horizonte-Conceição do Mato Dentro Highway, 4 Nov. 1972, *A.B. Joly & J. Semir CFSC 3685* (K, MBM, SP, UEC).

8. Symplocos microstyla Aranha, P.W. Fritsch, and Almeda, Proc. Calif. Acad. Sci. 56:299–301. 2005. Type.— Brazil. Minas Gerais: Serra do Caraça, Parque do Caraça on the trail to Pico do Inficcionado, 1941 m, 20°08′S, 43°27′W, 18 November 2004, *F. Almeda, P.W. Fritsch, J.L.M. Aranha Filho & R. Belinello 8878* (holotype: UEC!; photo of holotype: MBM!; isotypes: BHCB!, CAS!, ESA!, K!, MO!, NY!, SP!, SPF!, US!).

Tree ca. 3 m tall. Branches subquadrangular, striate, fissured, golden yellow-tomentose, glabrescent. Petiole 1–4 mm long, adaxially concave, sparsely golden yellow-tomentose, glabrescent; leaf blade elliptic, oblong, obovate, ovate, or rarely rotund, 0.5–3.5 × 0.3–1.6 cm, abaxially golden yellow-tomentose, glabrescent, adaxially sparsely puberulent on basal half of midvein, otherwise glabrous, glabrescent, secondary and tertiary veins highly branched near midvein and margin, base cuneate or subrounded, margin entire, marginal glands lacking, apex obtuse, retuse, or rarely subacute, apical gland usually present, early caducous. Inflorescence 3.5–5 mm long, 1-flowered; bracts 7 to 15, sparsely to densely golden yellow-tomentose mainly abaxial-medially; the two basal bracts usually caducous, deltoid or subdeltoid, keeled, 1–1.5 × 0.5–0.75 mm, margin not ciliate, apex acute or nearly so, apical gland usually lacking; other bracts 0.8–1.5 × 1–2 mm, margin

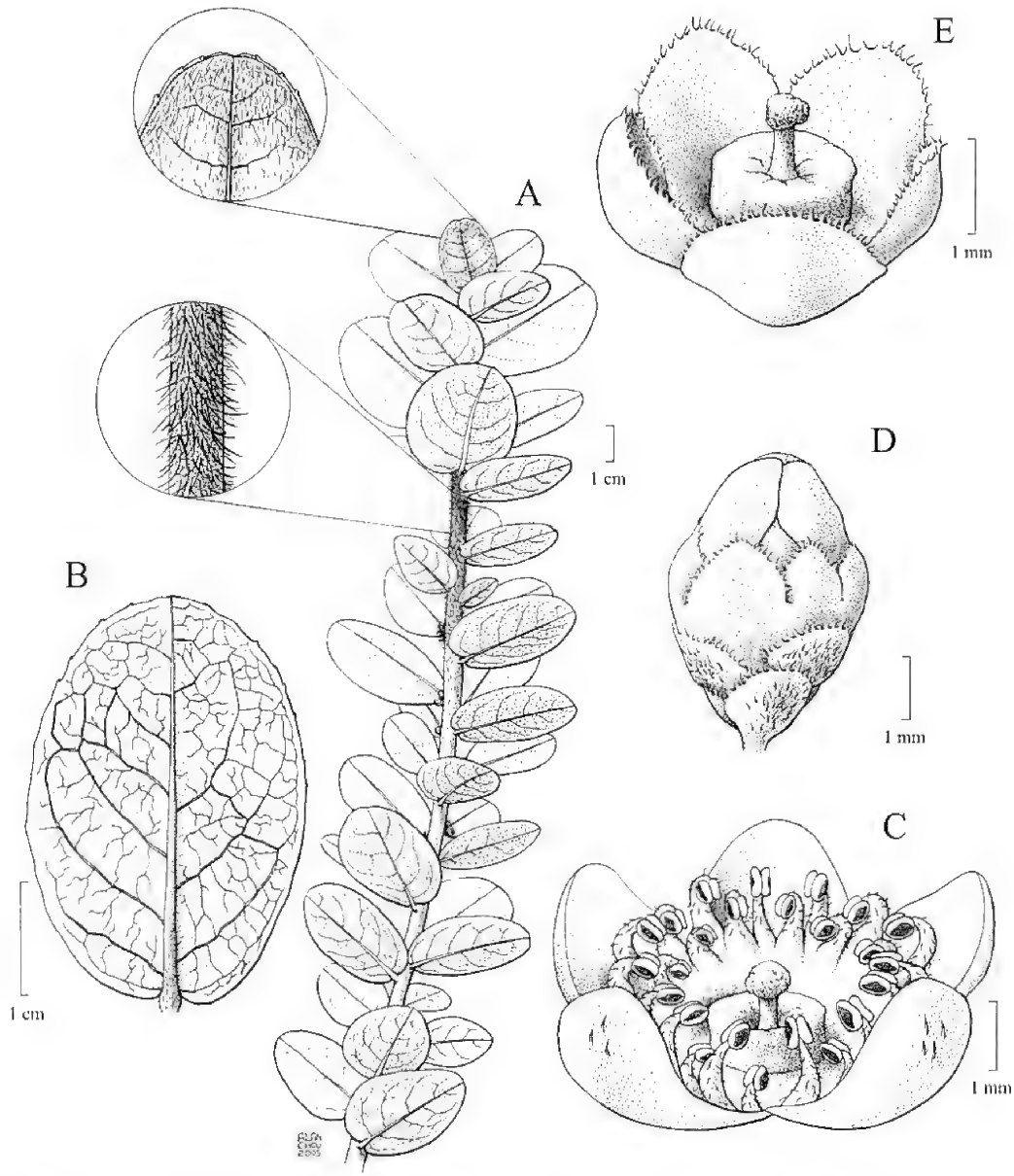

FIGURE 11. *Symplocos insolita* Aranha, P.W. Fritsch, and Almeda. A. Flowering branch with cauline and leaf indument detail; B. Representative leaf (abaxial surface); C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud and subtending bracts; E. Flower with corolla and androecium removed. (A–B from *Joly & Semir CFSC 3685*; C–E from *Almeda et al. 8910*).

ciliate, apices of basalmost obtuse, gradually more rounded distally. Flower 3–4 mm long; hypanthium 0.4–0.5 mm long, glabrous; calyx lobes subdeltoid or less often subrotund, 0.5–1 × 0.6–0.8 mm, golden yellow-tomentose mainly abaxial-medially; corolla lobes 5, ascending, pale green, broadly elliptic to ovate, 1.5–2 × 0.8–1 mm, glabrous. Stamens 25 to 30(to 35), exceeding and obscuring gynoecium; filaments 0.5–1.1 mm long; anthers yellow. Disc 0.5–0.7 mm in diameter, flat, rugose, glabrous; style ca. 0.1 mm long, glabrous. Fruit (2)3-locular, globose or occasionally

ellipsoid or ovoid, 2–4 × 1–3 mm, disc not enlarged and not distended beyond persistent calyx; calyx lobes slightly appressed to disc, sparsely golden yellow-tomentose. Seed 1(2), ca. 2–3 × 0.5–1 mm.

Vernacular name.— None.

Illustration.— Figure 12.

Phenology.— Flowering and fruiting in November.

Distribution and habitat.— *Symplocos microstyla* is known only from Pico do Inficcionado in the Serra do Caraça and represented by two individuals. It grows among *Ilex* in campo rupestre at ca. 1950 m elevation. Distribution map, Figure 4.

Discussion.— *Symplocos microstyla* is recognized by the combination of its eglandular, tomentose (when young) leaves abaxially, ascending corolla lobes, pale green stamens exceeding and obscuring the gynoecium, 0.1 mm-long style, and 2–4 × 1–3-mm fruit with tomentose calyx lobes. It is similar to *S. organensis* in habit and leaf size and shape. *Symplocos organensis* differs from *S. microstyla* by its glabrous leaves, basally lavender and distally white corolla lobes that are

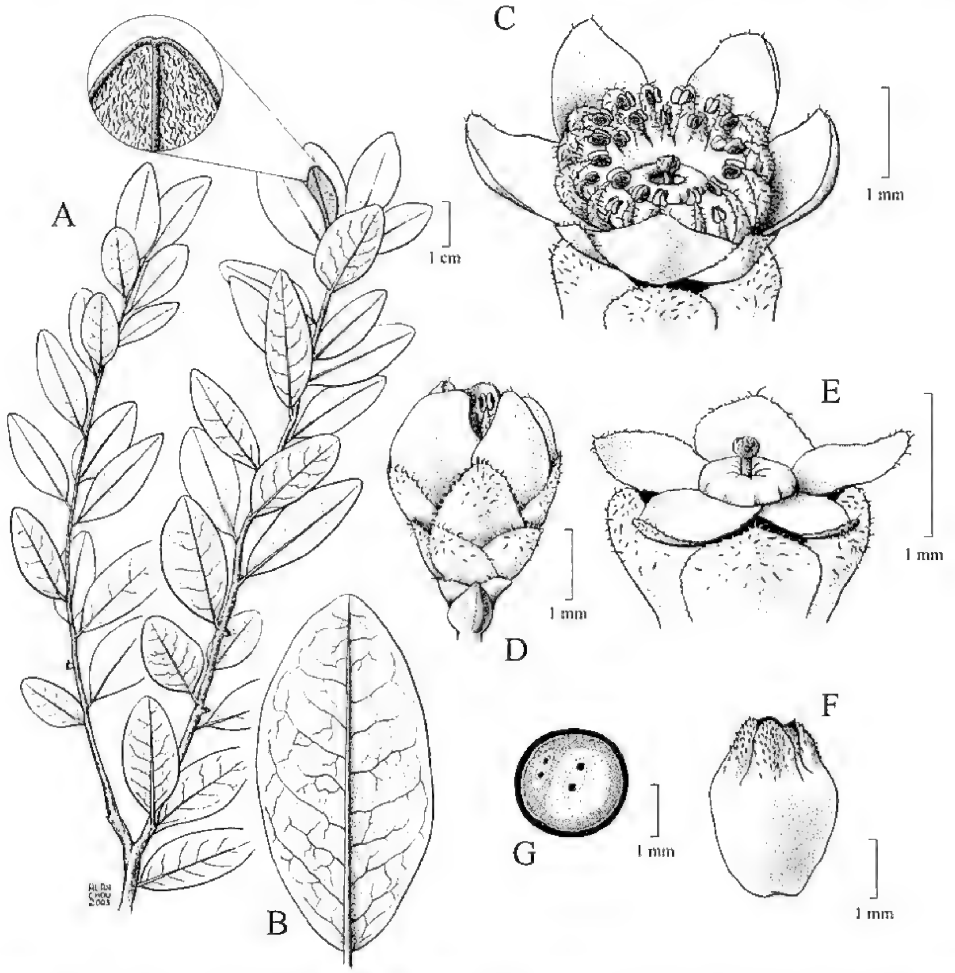

Figure 12. *Symplocos microstyla* Aranha, P.W. Fritsch, and Almeda. A. Flowering branch with leaf indument detail; B. Representative leaf (abaxial surface); C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud and subtending bracts; E. Flower with corolla and androecium removed; F. Mature fruit; G. Mature fruit in cross-section. (A–G from *Almeda et al. 8878*).

arched and spreading outwardly, stamens exceeding but not obscuring the gynoecium, style greater than 0.5 mm, and 7–12 × 5–7-mm fruit.

Additional specimens examined.— Brazil. Minas Gerais: Catas Altas, Serra do Caraça, Pico do Inficcionado, 25 Nov. 1999, *M.F. de Vasconcellos s.n.* (BHCB 52572); no location indicated, Serra do Caraça, Morro do Inficcionado, 1883, *A.F.M. Glaziou 15202* (K).

9. Symplocos nitidiflora Brand in Engl., Pflanzenr. IV. 242 (6):71. 1901. Type.— Brazil. "São Paulo" (protologue), no date indicated, *F. Sellow 221* (holotype: B destroyed; lectotype, here designated: K!).

Brand (1901) proposed the name *Symplocos nitidiflora* based on *Sellow 221* and *770*. Only *Sellow 221* from K has been seen by us and therefore we selected this material as lectotype.

Tree 2–9 m tall. Branches distally flattened, smooth, sparsely white- or golden yellow-strigillose, glabrescent. Petiole 13–20 mm long, adaxially concave to canaliculate, sparsely white- or golden yellow-strigose, glabrescent; leaf blade obovate or less often oblanceolate or elliptic, 5–16 × 2–5 cm, abaxially white- or golden yellow-strigillose, glabrescent, adaxially sparsely puberulent on basal half of midvein, otherwise glabrous, secondary and tertiary veins sparsely branched near midvein and highly branched near margin, base attenuate or nearly so, margin entire or inconspicuously serrulate-crenate on distal half, marginal and apical glands usually early caducous, persistent glands 0 to 8 per cm, apex acuminate or occasionally obtuse, acumen (when present) 2–7 mm long. Inflorescence 5–20 mm long, 1- to 20-flowered; bracts 7 to numerous, densely white- or golden yellow-strigillose abaxially; the two basal bracts usually early caducous, rotund, keeled to concave, 3–4 × 1.3–2.5 mm, margin not ciliate, apex rounded or nearly so, apical gland usually lacking; other bracts 1–2 × 1–2 mm, apices acute to obtuse. Flower 3–7 mm long; hypanthium 1–1.5 mm long, densely white- or golden yellow-strigillose, rarely glabrous; calyx lobes 5, subdeltoid, 1–1.8 x 1–1.3 mm, densely white- or golden yellow-strigillose abaxially, margin ciliate; corolla lobes 5(6), reflexed, green or rarely white to greenish white, elliptic to subrotund, 3–5 × 2.2–3.5 mm, densely white- or golden yellow-strigillose abaxially. Stamens (20 to)30 to 35, exceeding and obscuring gynoecium; filaments 0.5–5 mm long; anthers yellow. Disc 1–1.5 mm in diameter, flat, rugose, pilose, rarely glabrous; style 1–1.5 mm long, usually glabrous. Fruit (2–)3-locular, ellipsoid, 10–20 × 5–10 mm, disc not enlarged and not distended beyond persistent calyx; calyx lobes tightly appressed to disc, densely white- or golden yellow-strigillose. Seed 1 or 2(3), 6–7 × 0.9–1.3 mm.

Vernacular name.— caporoca falsa (Bidá 1995).

Illustration.— Figure 14.

Photographic images.— Figures 1E, 1F.

Phenology.— Flowering mostly from September to November, occasionally June to August; fruiting mostly from January to March, occasionally May or October to November.

Distribution and habitat.— *Symplocos nitidiflora* occurs mainly in the Serra do Mar (Mata Atlântica) of Paraná, reaching northern Rio de Janeiro. It grows mainly in low montane ombrophilous forest (890 to 1000 m elevation) as a mid-canopy tree. It is also found in high montane ombrophilous forest, transitional habitats between montane ombrophilous and araucaria forest, or less often in riparian situations (ca. 1050 to 1200 m elevation) where it can be a small tree. In São Paulo, this species reaches the western regions of the Serra do Mar, where it occurs in low montane ombrophilous forest. Distribution map, Figure 13.

Discussion.— *Symplocos nitidiflora* is characterized by the combination of its strigillose leaves (when young) abaxially, strigillose calyx lobes, strongly reflexed and densely strigillose corolla lobes abaxially, yellow anthers, and fruit 10–20 mm long. Based on leaf size and shape, we hypothesize that *S. nitidiflora* is related to *S. altissima* and *S. falcata*. *Symplocos altissima* is distin-

guished from *S. nitidiflora* by its glabrous leaves. *Symplocos falcata* can be distinguished from *S. nitidiflora* by its ascending or spreading corolla lobes and white to greenish white anthers, and pollen (see discussion under *S. falcata*).

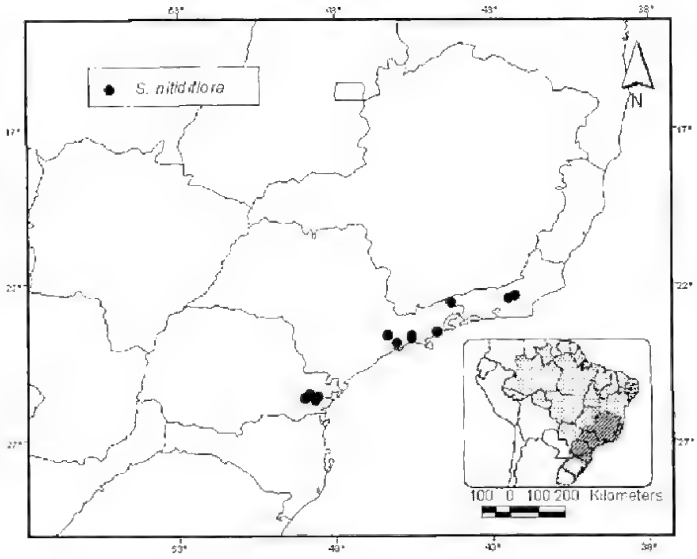

FIGURE 13. Distribution of *Symplocos nitidiflora*.

ADDITIONAL SPECIMENS EXAMINED.— BRAZIL. Paraná: Morretes, Serra do Mar, Graciosa Road, near Caminho dos Jesuítas, 28 Oct. 1990, *A. Bidá 636* (MBM, NY, UPCB); Serra do Mar, Graciosa-Caminho dos Jesuítas, 23 Mar. 1990, *A. Bidá 650* (UPCB); Piraquara, Serra do Mar, Carvalho, 13 Sep. 1911, *P.K.H. Dusen 13001* (NY, S (3)); road to and vicinity of SANEPAR Water Company, 500 m from Represa Carvalhinho, 17 Oct. 2005, *P.W. Fritsch & J.L.M. Aranha Filho 1823* (CAS, MBM, UEC); 5 Nov. 2001, *R. Goldenberg 521* (UPCB); Mananciais da Serra, 1 Oct. 2004, *R. Goldenberg & M. Reginatto 669* (UPCB); Mananciais da Serra, Feb. 2004, *R. Goldenberg & I.G. Varassin 617* (UPCB); Banhado, Rio Taquari, 29 Nov. 1951, *G. Hatschbach s.n.* (MBM 23462); 2 Nov. 1948, *G. Hatschbach 1085* (MBM, RFA, S, SP); Quatro Barras, Serra do Mar, Graciosa Road, 23 May 1990, *A.C. Cervi 3117* (UPCB); São José dos Pinhais, Purgatório, 10 Sep. 1982, *G. Hatschbach 45289* (MBM, NY); Santo Andrade Colony, 10 Aug. 1984, *G. Hatschbach 48990* (G, MBM, NY, UEC). **Rio de Janeiro:** Nova Friburgo, Mury, Macaé de Cima, 25 Oct. 1986, *G. Martinelli & M. Leitman 11819* (UPCB); Macaé de Cima, Sophronites Farm, Rio Flores , 20 Aug. 1987, *S.V.A. Pessoa et al. 281* (UPCB); Parque Nacional da Serra dos Órgãos, 16 Oct. 1942, *D. de Barros 1051* (RB); Visconde de Mauá, Serra do Itatiaia, Ribeirão Bonito, 23 June 1936, *P. Campos Porto & L. Lanstyak 2936* (RB); Serra do Itatiaia, Ribeirão Bonito, 20 June 1936, *L. Raristyak 105* (B); no location indicated, 1891, *A.F.M. Glaziou 18347* (K); 1863, *L. Neto 290* (R). **São Paulo:** Salesópolis, Casa Grande, Estação Biológica da Boracéia, 17 Dec. 1986, *A. Custódio Filho 2801* (UEC); Boracéa, 30 Jan. 1949, *M. Kuhlmann 1777* (SP); Santo André, Alto da Serra, *N. de Andrade s.n.* (R 1554); São Paulo, Jabaquara, 12 Oct. 1933, *O. Handro s.n.* (ESA 87706, SP 58585); Jardim Botânico, 21 Sep. 1931, *F.C. Hoehne s.n.* (G 16272); Jardim Botânico (Parque do Estado), 23 Sep. 1931, *F.C. Hoehne s.n.* (GUA 20290, MBM 69154, NY 486873, SP 28275, UEC 23244); Ubatuba, Estação Experimental do Instituto Agronômico, 12 Aug. 1977, *P.E. Gibbs & H. de F. Leitão Filho 5635* (BM, MBM, NY, R, UEC); no location indicated, *F.C. Hoehne 28275* (NY (2), S (2)). No location indicated, 1840, *H.F. Talbot s.n.* (K 1978113).

10. Symplocos organensis Brand in Engl., Pflanzenr. IV. 242 (6):72. 1901. TYPE.— BRAZIL. Rio de Janeiro: Serra dos Órgãos, 8 October 1869, *A.F.M. Glaziou 3641* (holotype: B destroyed; lectotype, here designated: NY!; isolectotypes: K!, P).

Symplocos organensis was proposed by Brand (1901) from *Glaziou 3641*, *6023*, *15202*, and *17130*. Aranha Filho et al. (2005) excluded *Glaziou 15202* from the syntypes of *S. organensis* and cited it as a paratype of *S. microstyla*. We selected *Glaziou 3641* from NY because it comprises a single sheet, has a precise date and locality, and has good flowering material.

Shrub or occasionally small tree 1–3 m tall. Branches subquadrangular, striate, fissured, glabrous. Petiole 1–6 mm long, adaxially concave, glabrous; leaf blade obovate, less often oblong,

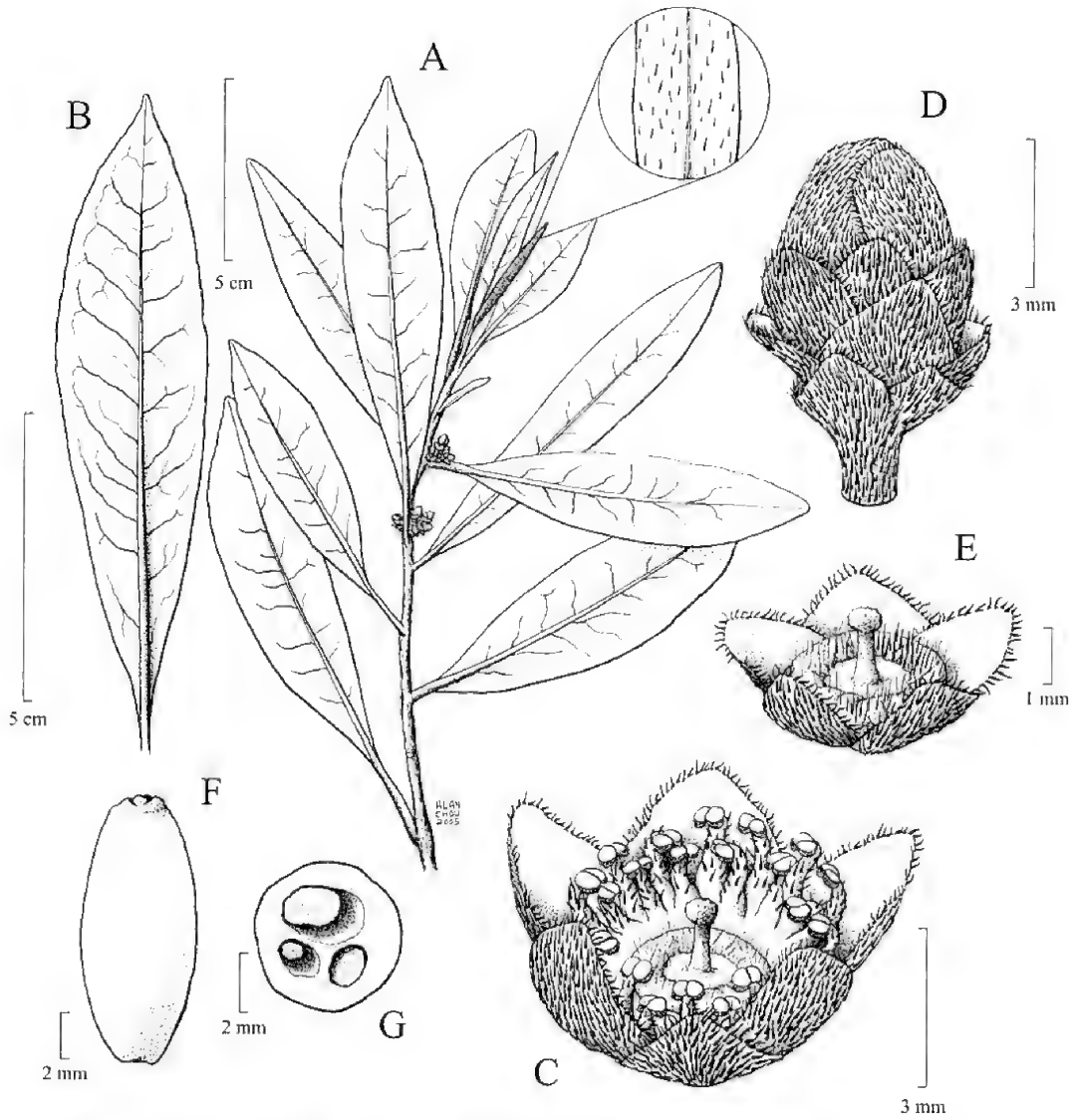

FIGURE 14. *Symplocos nitidiflora* Brand. A. Flowering branch with leaf indument detail; B. Representative leaf (abaxial surface); C. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; D. Flower bud and subtending bracts; E. Flower with corolla and androecium removed; F. Mature fruit; G. Mature fruit in cross-section. (A–B from *Sellow 221*; C–E from *Hoehne 28275*; F–G from *Kuhlmann 1777*).

ovate or elliptic, 2–4.5 × 0.5–1.5 cm, glabrous except at base and around apical gland when young abaxially, then glabrescent, secondary and tertiary veins sparsely branched near midvein and margin, base attenuate or occasionally cuneate to rounded, margin entire or less often inconspicuously serrulate on distal half, marginal and apical glands usually early caducous, persistent glands 0 to 8 per cm, apex obtuse, retuse, or rarely subacute. Inflorescence 5–10 mm long, 1- to 4-flowered; bracts 7 to 20, glabrous; the two basal bracts usually early caducous, deltoid or subdeltoid, keeled, 1.5–2 × 1–1.5 mm, margin not ciliate, apex acute or subacute, apical gland usually present; other bracts 1–2 × 1–2.5 mm, apices of basalmost obtuse, gradually more rounded distally, margin cili-

ate. Flower 4–11 mm long; hypanthium 0.5–1 mm long, glabrous; calyx lobes rotund or subrotund, 1.5–2 × 1–1.5 mm, glabrous; corolla lobes 5 to 8, arched-spreading, basally lavender and distally white, elliptic to obovate, 2.7–3.5 × 1.7–2 mm, glabrous. Stamens 20 to 25(to 30), exceeding but not obscuring gynoecium; filaments 0.5–2 mm long; anthers yellow. Disc 1–1.5 mm in diameter, flat, smooth, glabrous; style 0.8–1 mm long, glabrous. Fruit (1)2(3)-locular, ellipsoid or rarely subovoid, 7–12 × 5–7 mm, disc not enlarged and not distended beyond persistent calyx; calyx lobes tightly appressed to disc, glabrous. Seed 1(2), 5–8 × 1–2 mm.

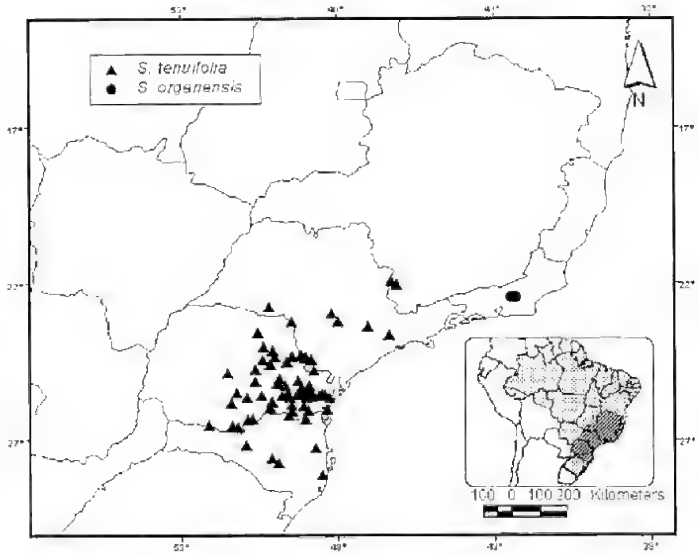

FIGURE 15. Distribution of *Symplocos organensis* and *S. tenuifolia*.

VERNACULAR NAME.— None.

ILLUSTRATION.— Figure 16.

PHOTOGRAPHIC IMAGES.— Figures 1G, 1H.

PHENOLOGY.— Flowering in October to November; fruiting in November.

DISTRIBUTION AND HABITAT.— Endemic to the Serra dos Órgãos at ca. 2000 m elevation, where it occurs in elfin forest as a shrub or small tree. Distribution map, Figure 15.

DISCUSSION.— *Symplocos organensis* is recognized by the combination of its glabrous leaves, arched and spreading corolla lobes that are distally white and basally lavender, stamens that exceed but do not obscure the gynoecium, 0.8–1 mm-long style, and 7–12 × 5–7 mm-long fruit. *Symplocos organensis* is similar to *S. microstyla* in leaf shape and size, and habit. *Symplocos microstyla* has tomentose leaves when young abaxially, tomentose calyx lobes, corolla lobes pale green, ascending, stamens obscuring the gynoecium, stigma nearly sessile (style ca. 1 mm long), and fruit 2–4 × 1–3 mm.

ADDITIONAL SPECIMENS EXAMINED.— **BRAZIL. Rio de Janeiro:** Nova Friburgo, Serra do Mar, Pico Caledônia, 11 Nov. 2004, *F. Almeda et al. 8792* (CAS, UEC); Serra do Mar, Pico Caledônia, 11 Nov. 2004, *F. Almeda et al. 8798* (CAS, UEC); Serra dos Órgãos, 19 Oct. 1958, *A.G. Andrade 152* (R, UPCB); Abrigo 4, 19 Oct. 1958, *M. Emmerich 138* (R); Pedra Açu, 21 Oct. 1872, *A.F.M. Glaziou 6023* (BM, G, K, NY, RFA); *A.F.M. Glaziou 17130* (K).

11. Symplocos tenuifolia Brand in Engl., Pflanzenr. IV. 242 (6):71–72. 1901. TYPE.— BRAZIL. Paraná: "Carambeí" (protologue), no date indicated, *F. Sellow 4806* (holotype: B destroyed; lectotype, here designated: K!).

Brand (1901) designated several syntypes when describing *S. tenuifolia*: *Lindberg 506*, *Regnell II40*, *Sellow B 2262*, *c 2303*, *417*, *4806*, *Ule 1093*, and *Widgren 1157½*. We choose *Sellow 4806* at K as lectotype even though it does not indicate locality and date because it has a label indicating that it is a duplicate from B. Thus it is likely to have been seen by Brand.

Tree or occasionally shrub 1.5–15 m tall. Branches ± terete, striate, fissured, densely white-,

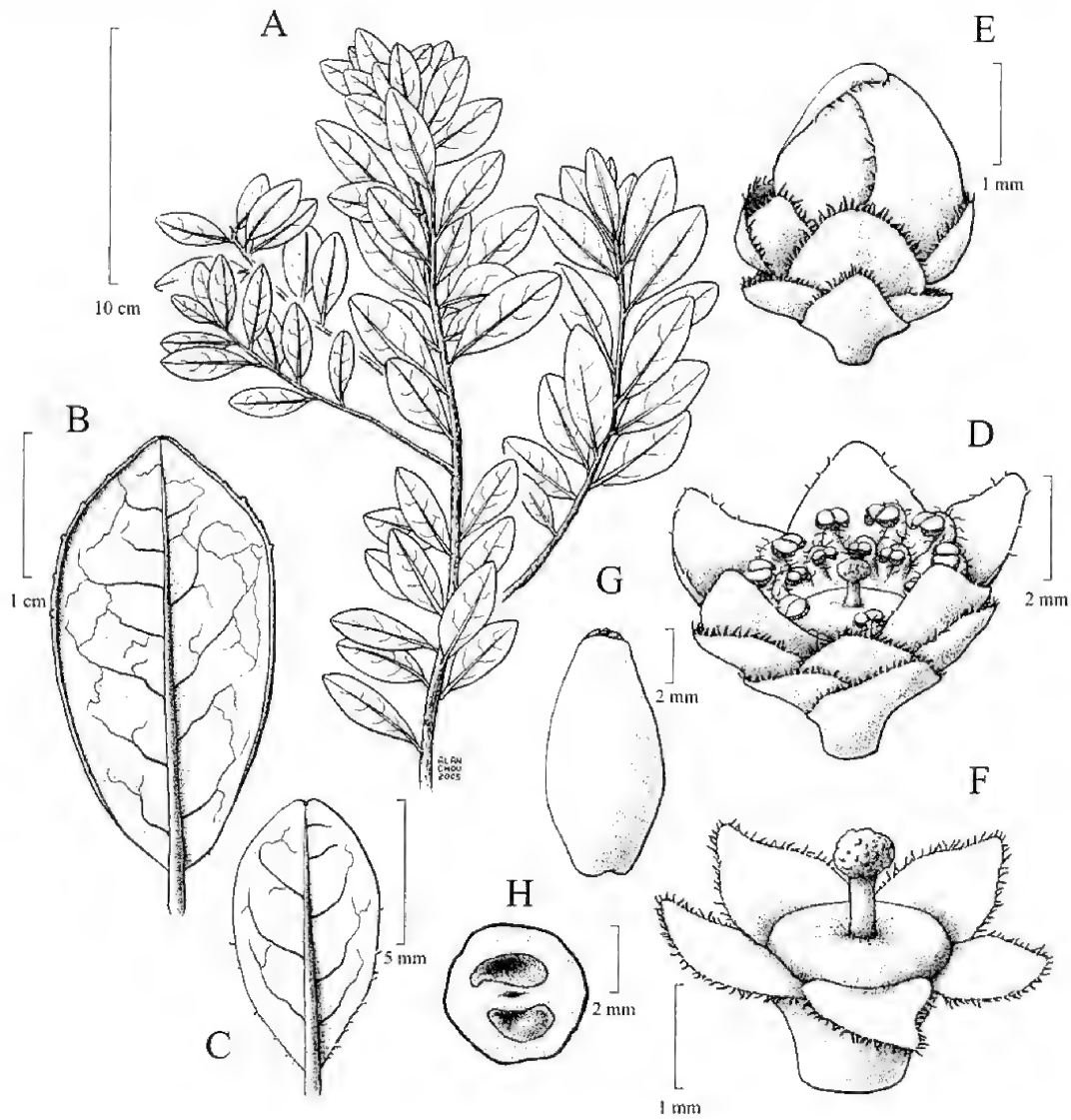

FIGURE 16. *Symplocos organensis* Brand. A. Flowering branch; B. Representative mature leaf (abaxial surface); C. Representative young leaf (abaxial surface); D. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; E. Flower bud and subtending bracts; F. Flower with corolla and androecium removed; G. Mature fruit; H. Mature fruit in cross-section (A–C from *Glaziou 3641*; D–H from *Almeda et al. 8798*).

golden yellow-, or ferrugineous-tomentose-strigillose, glabrescent. Petiole 2–5 mm long, adaxially flattened or slightly concave, sparsely white- or golden yellow-tomentose-pilose, glabrescent; leaf blade elliptic to narrowly elliptic, 2–9 × 0.6–2.5 cm, abaxially mixed white-, golden yellow-, or ferrugineous-tomentose (mainly near margin) and sericeous-pilose otherwise, glabrescent, adaxially occasionally sparsely white-, golden yellow-, or ferrugineous-sericeous-strigose on surface, densely sericeous or pilose along midvein, glabrescent, secondary and tertiary veins highly branched near midvein and margin, base attenuate or cuneate, margin entire or occasionally inconspicuously serrulate on distal half, marginal and apical glands usually caducous, persistent glands 0 to 8 per cm,

apex acuminate or occasionally acute, acumen (when present) 2–15 mm long. Inflorescence 2.5–5 mm long, 1- to 10-flowered; bracts 6–22; the two basal bracts usually early caducous, deltoid to subrotund, keeled, 0.7–1.1 × 0.5–0.8 mm, glabrous, occasionally white-, golden yellow-, or ferrugineous-tomentose abaxially, margin not ciliate, apex acute or nearly so, apical gland usually lacking; other bracts 1–1.5 × 1–1.5 mm, white-, golden yellow-, or ferrugineous-tomentose abaxially, margin ciliate, apices of basalmost obtuse to rounded, gradually more rounded distally. Flower 2–3.5 mm long; hypanthium 0.8–1 mm long, glabrous; calyx lobes deltoid to rotund, 1–1.5 × 1–1.5 mm, glabrous or rarely golden yellow- or ferrugineous-tomentose abaxial-medially, then glabrescent; corolla lobes 5(6), green, white, or greenish white, broadly elliptic to obovate, 2–3 × 1–1.8 mm, glabrous or rarely sparsely pubescent abaxially. Stamens 25 to 35, exceeding and obscuring gynoecium; filaments 0.5–1.8 mm long. Disc 0.8–1.2 mm in diameter, flat, ± rugose, glabrous; style 0.5–0.8 mm long, glabrous. Fruit 2(3)-locular, ovoid or less often globose, 3–6 × 4–5 mm, disc rarely slightly enlarged and slightly distended beyond persistent calyx; calyx lobes glabrous or rarely sparsely tomentose, slightly appressed to disc or occasionally erect. Seed 1 or 2, 2–5.5 × 1.5–3 mm.

VERNACULAR NAMES.— caporoca (*A.E. Biank 24* (MBM)), caporoquinha (*R.R.B. Negrelle et al. 610* (UPCB)), carne de vaca (*Beatriz 3* (MBM)), congonha (*P. Occhioni 5338* (RFA)), maria mole (*R. Reitz 3216* (MBM)), maria mole miúda (*Y.S. Kuniyoshi & Ponciano 4717* (MBM)), orelha de gato (*R. Reitz s.n.* (MBM)), pessegueiro-bravo (*A.L. Cavalheiro et al. s.n.* (SP)), and vauvú (*S.R. Ziller & Y.S. Kuniyoshi 713* (MBM)).

ILLUSTRATION.— Figure 17.

PHENOLOGY.— Flowering mostly from October to December, rarely September to May; fruiting mostly from December to March, rarely November, April, or May.

DISTRIBUTION AND HABITAT.— *Symplocos tenuifolia* is the most common and widespread species of section *Neosymplocos*. It is fairly common in Paraná, ranging to northern, central, and eastern Santa Catarina and southern Minas Gerais through southwestern and central São Paulo and rarely in the western regions of the Serra do Mar in São Paulo. *Symplocos tenuifolia* is commonly collected in araucaria forest (ca. 800 to 1100 m elevation). It is also fairly common in secondary vegetation, riparian situations, semideciduous forest and brejo, especially in transitional habitats between araucaria and montane ombrophilous forest (ca. 1300 m elevation). This species can also be encountered less commonly in restinga (sea level) from Santa Catarina to Paraná. One collection of *S. tenuifolia* was collected in a gallery forest surrounded by cerrado. Distribution map, Figure 15.

DISCUSSION.— *Symplocos tenuifolia* can be recognized by its vegetative characters. The midvein is densely sericeous or pilose (mostly in young leaves) and the leaf blade is mixed tomentose and sericeous-pilose, mainly tomentose near the margin and mainly sericeous-pilose otherwise. The margin of the young leaves is sparsely glandular (0 to 8 glands per cm). The dimensions of the mature fruit (3–6 × 4–5 mm) are also important diagnostic characters. Saplings of *S. tenuifolia* resemble those of *S. glandulosomarginata* in leaf size, shape, and indument. In *S. glandulosomarginata* the leaf margin is densely glandular (13 to 25 per cm). The only other species among *Neosymplocos* species that exhibits comparable foliar indument variation is *S. falcata*; the latter has larger fruits (8–10 mm long).

Bidá (1995) proposed *S. reitzii* in his Ph.D. thesis, but this name was never published. According to Bidá, *S. reitzii* would be endemic to eastern Santa Catarina state growing in montane ombrophilous forest (ca. 1000 m elevation) and would be morphologically similar to *S. tenuifolia*. Bidá (1995) differentiated *S. reitzii* from *S. tenuifolia* mostly based on branch indument, fruit shape, and calyx lobe size. Examining specimens of both entities, we could not determine if *S. reitzii* is

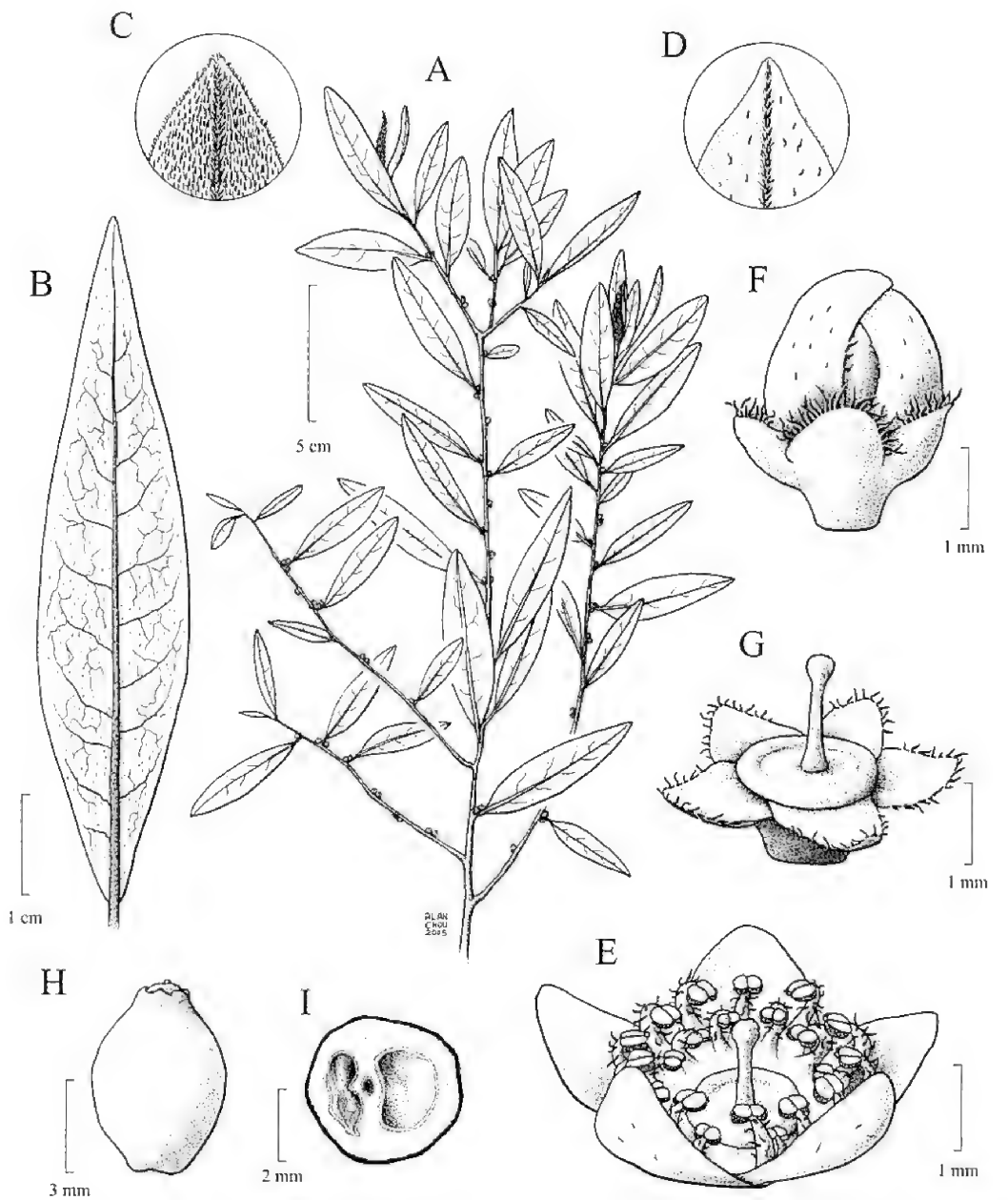

FIGURE 17. *Symplocos tenuifolia* Brand. A. Flowering branch; B. Representative leaf (abaxial surface); C. Leaf indument detail (abaxial surface); D. Leaf indument detail (adaxial surface); E. Flower at anthesis with androecium opened outward to show ovary apex, style, and stigma; F. Flower bud; G. Flower with corolla and androecium removed; H. Mature fruit; I. Mature fruit in cross-section (A–D from *Sellow 4806*; E–G from *Hatschbach 27614*; H–I from *Krapovickas & Cristóbal 40910*).

taxonomically distinct. Therefore, we tentatively consider *S. reitzii* to be the same as *S. tenuifolia*. Further field work will be needed to determine the status of *S. reitzii*.

ADDITIONAL SPECIMENS EXAMINED.— BRAZIL. Minas Gerais: Caldas, Nov. 1854, *G.A. Lindberg 506* (S); 5 Nov. 1873, *C.W.H. Mosen 619* (S (4)); 1 Mar. 1876, *C.W.H. Mosen 4533* (S (2)); *A.F. Regnell II40* (K,

M, NY (2), S (5)); *A.F. Regnell II40c* (S); Poços de Caldas, Chiqueirão Farm, *H. de F. Leitão Filho et al. 1586* (UEC); Dec. 1882, *C.B. Rolian 7472* (R); no location indicated, 1845, *J.F. Widgren 370* (S); 1845, *J.F. Widgren 1157½* (K, M, NY, S (2)). **Paraná:** Açungui, 1 Mar. 1948, *A. Mattos & L.G. Labouriau 2011* (RB); Adrianópolis, Mato Preto, 18 Jan. 2000, *O.S. Ribas & L.M. Abe 3024* (ESA, G, HRCB, MBM); Antonina, Rio do Meio, 26 Nov. 1982, *G. Hatschbach 45741* (BHCB, MBM, NY, UPCB); Monte Alegre, 23 Mar. 1954, *J.G. Kuhlmann s.n.* (RB 150802); Balsa Nova, Tamanduá, 12 Nov. 1980, *G. Hatschbach 43348* (MBM, NY); Biturana, Fomeado Grande Farm, 2 Feb. 2005, *D. Liebsch s.n.* (UPCB 50525); Bocaiúva do Sul, Sesmaria, Rio Capivari, 14 Jan. 1969, *G. Hatschbach 20737* (MBM, RFA); 5 Dec. 1978, *G. Hatschbach 41840* (MBM, NY, UPCB); Colony São João XXIII, 26 Nov. 1986, *G. Hatschbach & J. Cordeiro 50814* (HRCB, MBM, S, UPCB); road to Parque das Lauráceas, near Colony São João, 13 Nov. 1993, *C.B. Poliquesi & J. Cordeiro 163* (ESA, MBM, UEC, UPCB); Campo Largo, Retiro Grande, 3 Jan. 1978, *G. Hatschbach 40722* (MBM, UEC); Campo Magro, Caverna Sumidouro, 18 Nov. 1996, *G. Tiepolo & A.C. Svolenski 600* (MBM); Campo do Tenente, Campo de Fora Farm, 10 Feb. 1982, *R. Kummrow & J.G. Stutts 1730* (MBM); Carambeí, Rio São João, Castro, 17 Dec. 1975, *R. Reitz & R.M. Klein 17849* (B, NY); Clevelândia, 3 Capões, 22 Oct. 1972, *G. Hatschbach 30808* (MBM, RFA); Brandalize Farm, 29 Apr. 1966, *J.C. Lindeman & J.H. de Haas 1096* (MBM); Colombo, EMBRAPA, 15 Dec. 1978, *P. Carvalho 96* (MBM); Campestre, 15 Dec. 1989, *V. Nicolack & O.S. Ribas 110* (MBM, UEC); 24 Sep. 2004, *R.F.S. Possette & M. Dias 265* (MBM); EMBRAPA, Rio Ribeira, 15 Dec. 1978, *E. Rotta s.n.* (MBM 65724); Contenda, near Contenda, 7 Nov. 1977, *L.R. Landrum 2430* (MBM); Curitiba, UFPR, Centro Politécnico, trail to Educação Física, 29 Nov. 1992, *A. Bidá 677* (UPCB); UFPR, Centro Politécnico, 12 Dec. 1992, *A. Bidá 678* (UPCB); ca. 300 m from the Centro de Ciências Florestais e da Madeira, UFPR, 20 m off the road to the Centro, 14 Oct. 2005, *P.W. Fritsch & J.L.M. Aranha Filho 1803* (CAS, UEC); 4 Apr. 1914, *I.G. Jönsson 4* (S); 4 Apr. 1914, *I.G. Jönsson 132* (NY); Rio Taquari, 12 Nov. 1961, *E. Pereira 6886* (RB); General Carneiro, Passo da Galinha, 19 Nov. 1972, *G. Hatschbach 30714* (MBM, NY, RFA, SP, UEC); Guapira, 16 Feb. 1913, *A.C. Brade 5802* (S (2), SP); Guaratuba, Rio da Praia, 22 Nov. 1967, *G. Hatschbach 17941* (MBM (2), NY, RFA, UPCB); Inácio Martins, Monte Alto, 21 Jan. 1998, *G. Hatschbach & et al. 67499* (ESA, MBM); Irati, Aleixo Farm, 31 Oct. 1972, *P. Carvalho 84* (MBM, UEC); Colégio Estadual Florestal de Irati, 14 Mar. 1973, *P. Carvalho 171* (MBM); Itaiacoca, 18 Mar. 1904, *P.K.H. Dusen s.n.* (S); Itaperussu, 18 Nov. 1908, *P.K.H. Dusen 7152* (NY, S); Itapoá, Reserva Volta Velha, Jan. 1992, *R.R.B. Negrelle s.n.* (UPCB 21359); Reserva Volta Velha, 17 Feb. 1993, *R.R.B. Negrelle & C. Londero A762* (MBM, UPCB); Reserva Volta Velha, 11 Jan. 1992, *R.R.B. Negrelle et al. 28* (UPCB); Reserva Volta Velha, 20 Jan. 1993, *R.R.B. Negrelle et al. 610* (UPCB); Reserva Volta Velha, 22 Nov. 1996, *C.I. Salimon s.n.* (UPCB 28971); Ivaí, 10 Mar. 1977, *G. Hatschbach 39788* (MBM, UEC); Jaguariaíva, Rio das Mortes, 2 Nov. 1989, *A.C. Cervi 2990* (MBM (2), UPCB); Rio das Mortes, 23 Oct. 1990, *A.C. Cervi & A. Dunaiski 3279* (NY, SJRP, UPCB); Parque Estadual do Cerrado, 28 Oct. 1993, *A.C. Cervi & A. Uhlmann 4149* (UPCB); PR-151, near the bridge over Rio das Mortes, 16 Dec. 1991, *A.C. Cervi et al. 3587* (MBM, UPCB); 28 May 1997, *A.C. Cervi et al. 6272* (UPCB); 12 Apr. 1910, *P.K.H. Dusen 9691* (S); Jaguariaíva State Park, 16 Oct. 2005, *P.W. Fritsch et al. 1822* (CAS, UEC); Água Clara, 12 Nov. 1981, *G. Hatschbach 44366* (MBM, RB); Recanto Prainha, 10 Feb. 1997, *O.S. Ribas & L.B.S. Pereira 1716* (BHCB, SJRP, UPCB); Parque Estadual do Cerrado, 19 July 1994, *A. Uhlmann s.n.* (UPCB 25784); Lapa, Volta Grande, 20 Dec. 1979, *P.I. Oliveira 180* (B, MBM); PR-427, 1 km from the bridge over Rio Iguaçu, 29 Nov. 2001, *O.S. Ribas et al. 3961* (BHCB); Mandirituba, Passo Amarelo, 21 Sep. 1992, *A. Dunaiski 303* (MBM); Morretes, Barro Branco, 29 Jan. 1987, *J. Cordeiro & A. Souza 411* (MBM, S); Rio Sapintanduva, 25 Jan. 1977, *G. Hatschbach 39726* (MBM); Otacílio Costa, Cardoso Farm, 10 Feb. 1996, *O.S. Ribas et al. 1205* (MBM); Palmeira, Colony Quero-Quero, 10 Nov. 1951, *G. Hatschbach 2690* (MBM, UPCB); Santa Amélia Farm, 5 Nov. 1967, *G. Hatschbach & J.P. Fontella 17691* (GUA, MBM RB); Santa Rita Farm, ca. 65 km W of Curitiba on road to Ponta Grossa, 2 Dec. 1981, *L.R. Landrum 3928* (CAS, MBM); Paranaguá, Areal Imbocuí, 18 Apr. 1995, *S.R. Ziller & Y.S. Kuniyoshi 713* (MBM); Banestado, near Praia Leste, 25 Nov. 1994, *S.R. Ziller & G. Wanke 615* (MBM); Paula Freitas, 17 Nov. 1972, *G. Hatschbach & C. Koczicki 30699* (MBM, RFA); Pinhais, 1 Oct. 1910, *P.K.H. Dusen 10331* (K, NY, S); 12 Feb. 1914, *P.K.H. Dusen 14512* (S); 3 Nov. 1914, *P.K.H. Dusen 15801* (K, NY, S); Pinhão, Rio Touros, 10 Mar. 1967, *J.C. Lindeman & J.H. de Haas 4748* (MBM, NY); Barbaquá, *J.C. Lindeman & J.H. de Haas 4917* (MBM, RB); Piraí do Sul, Joaquim Murtinho, 18 Dec. 1976, *G. Hatschbach 39198* (MBM, NY, UEC); Piraquara, Condomínio Cantareira, 31 May 2001, *O.V. Doria 39* (ESA); 1908, *P.K.H. Dusen 6897* (S); Serra

do Mar, along road to Morro do Canal, ca. 8 km from BR-277, 15 Oct. 2005, *P.W. Fritsch & J.L.M. Aranha Filho 1813* (CAS, MBM, UEC); Florestal, 26 Dec. 1947, *G. Hatschbach s.n.* (MBM 23497); road between Rio Taquari and Rio Divisa, 13 Nov. 1949, *G. Hatschbach 1611* (MBM, RFA, S); Colony Santa Maria, Serra do Mar, 3 Oct. 1971, *G. Hatschbach 27614* (HB, MBM, RFA, S); Fazenda Experimental de Agronomia, 31 Mar. 1971, *N. Imaguirre 2775* (MBM); Mananciais da Serra, 14 Nov. 1983, *Y.S. Kuniyoshi & Ponciano 4717* (HB, MBM (3), SJRP); Mananciais da Serra Morro do Canal, 13 Nov. 1998, *A. Lacerda 100* (MBM, UPCB); Mananciais da Serra, Morro do Canal, 17 Dec. 1998, *A. Lacerda 192* (MBM, UPCB); Mananciais da Serra, 31 Oct. 1977, *L.R. Landrum 2244* (MBM); Colony Santa Luzia, 22 Nov. 1983, *P.I. Oliveira 780* (MBM, UPCB); Santa Bárbara Ranch, 14 Feb. 2004, *O.S. Ribas et al. 5888* (MBM, RB); 10 Mar. 1993, *A. Vicentini & S.R. Ziller 168* (MBM); Pitanga, 5 Mar. 2003, *A.E. Biank 24* (MBM); Ponta Grossa, 14 Nov. 1914, *P.K.H. Dusen 15858* (NY, S); Vale do Pitangui, 9 Nov. 1989, *A.C. Cervi & G. Hatschbach 3008* (CAS, MBM, UPCB); Parque Vila Velha, Lagoa Dourada, 23 Nov. 1963, *G. Hatschbach & E. Pereira 10719* (B); 2 Nov. 1928, *F.C. Hoehne s.n.* (SP 23301); Vila Velha, 16 Jan. 1987, *A. Krapovickas & C.L. Cristóbal 40910* (K, MBM); 24 Dec. 1971, *P.L. Krieger 11387* (RB); Café Highway, Lagoa Dourada, 26 Nov. 1972, *P. Occhioni 5371* (RFA); Vila Velha, Lagoa Dourada, 23 Nov. 1963, *E. Pereira & G. Hatschbach 8121* (HB, MBM, RB); Rio São Jorge, 6 Nov. 1992, *Takeda & Schiesinsky 904* (HRCB); Rio Tibagi, 20 Oct. 1999, *S.R. Ziller & W. Maschio 1942* (MBM); Porto Dom Pedro II, 22 Apr. 1911, *P.K.H. Dusen 11463* (NY, S); Quatro Barras, Pinhal, 25 Dec. 1943, *G. Hatschbach 82* (MBM, RB); Reserva, 13 Dec. 1996, *V.F. Kinupp et al. 257* (UEC, UPCB); Canguirí Farm, 9 Jan. 1984, *C.V. Roderjan & Y.S. Kuniyoshi 273* (MBM (2), UPCB); Serra da Baitaca, Morro Anhangava, 23 Jan. 1994, *G. Tiepolo 48* (MBM); 6 June 1995, *S.R. Ziller & W. Maschio 810* (MBM); São João do Triunfo, 7 Nov. 1967, *G. Hatschbach 17760* (B, MBM, UPCB); Fiat Lux Farm, W of São João do Triunfo, 21 July 1966, *J.C. Lindeman & J.H. de Haas 1874* (RB); São João Farm, 22 July 1966, *J.C. Lindeman & J.H. de Haas 1910* (MBM); 13 Oct. 1979, *G. Loughan s.n.* (MBM 65590, UPCB 11384); São José dos Pinhais, Contenda, 7 Nov. 1977, *G. Hatschbach 40298* (HB, MBM, NY, UEC); Colony Roseira, 23 Feb. 1968, *C. Koczicki 77* (MBM, NY (2)); road to Santa Catarina, 10 Feb. 1980, *Y.S. Kuniyoshi s.n.* (MBM 293196); BR-277, 21 Nov. 1984, *J.R.S. Muniz 3* (MBM); Barro Preto, 12 Jan. 1979, *P.I. Oliveira 154* (B, MBM, SPF); São Mateus do Sul, 9 Mar. 1929, *Gurgel s.n.* (R 111289, UPCB 3125); 6 Mar. 1929, *Gurgel & P. Occhioni 14648* (RB); *P.Nunes s.n.* (RFA 20547, 20620); Sapopema, Vila Rural, 15 Oct. 1998, *A.L. Cavalheiro et al. s.n.* (BHCB 50611, G); Telêmaco Borba, Parque Estadual Samuel Klabin, Recinto das Marrecas, Monte Alegre Farm, 1 Nov. 1994, *S.A. Filipaki s.n.* (UPCB 33131); Tibagi, Canyon Guartelá, 4 Nov. 1994, *C.M.V. Cardoso et al. s.n.* (ESA 49238, K 1978110, UEC 103733); Estrela Ranch, Rios Iapó-Saltinho, 12 Dec. 1989, *S. Colli et al. s.n.* (K 197863); Canyon Guartelá, Rio Iapó, near Cachoeira Ponte de Pedra, 10 Nov. 1992, *G. Hatschbach & E. Barbosa 58185* (BHCB, MBM); Canyon Guartelá, 10 Feb. 1997, *V.F. Kinupp 104* (G, SJRP); Parque Estadual do Guartelá, 29 Oct. 2004, *D.C. Maia & R. Morokawa s.n.* (UPCB 50231); Estiva, 11 Feb. 2004, *C.G. Mielke s.n.* (BHCB 60267); Parque Estadual do Guartelá, Rio Iapó, 20 Sep. 1996, *S.R. Ziller 1526* (MBM); Tijucas do Sul, Ambrósios, 27 Nov. 1990, *C.B. Poliquesi & J.M. Silva 31* (MBM); Ambrósios, 10 Jan. 1992, *O.S. Ribas & D. Guimarães 412* (MBM, UPCB); Ventania, Rancho dos Pinheiros, 9 Feb. 1999, *A.L. Cavalheiro et al. s.n.* (MBM 239764, SP 338664); Rancho do Pinheiro, 11 Dec. 1998, *E.M. Francisco & A.L. Cavalheiro s.n.* (SJRP 21688); no location indicated, Serrinha, 14 Jan. 1904, *P.K.H. Dusen 3436* (S); Capão Grande, 3 Feb. 1909, *P.K.H. Dusen 7745* (NY, S); near Brandalize Sawmill, ca. 20 km N of Clevelândia, 10 Apr. 1966, *J.C. Lindeman & J.C. de Haas 1090* (RB, MBM); BR-2, near Taquari, 50 km from Curitiba, Oct. 1971, *P. Occhioni s.n.* (RFA 13309); Rio Negro, 22 Nov. 1972, *P. Occhioni 5266* (RFA); Joinville-Curitiba Road, Km 47, 25 Nov. 1972, *P. Occhioni 5338* (RFA); BR-2, near Taquari, 50 km from Curitiba, 12 Nov. 1961, *G.J.F. Pabst & E. Pereira 6712* (HB, R, RFA); road between Ponta Grossa and Itararé, Km 203, 5 Nov. 1977, *G.J. Shepherd & J.B. de Andrade 6137* (MBM, RB, UEC). **Santa Catarina:** Bom Retiro, 25 Oct. 1957, *R. Reitz & R.M. Klein 5444* (NY); Brusque, Mata do Hoffmann, 25 Nov. 1949, *R. Reitz s.n.* (RFA 21845); Mata do Hoffmann, 25 Nov. 1949, *R. Reitz 3216* (B, G, HB, MBM, NY, S, UPCB); Azambuja, 9 Mar. 1954, *R. Reitz 5830* (NY, S (2)); Campo Alegre, lower slopes of Morro Iquererim, Sep. 1956, *L.B. Smith & R.M. Klein 8495* (NY, R); Lajes, ca. 15 km E of Otacílio Costa, 2 km W of the crest of Serra Geral, 21 Nov. 1977, *L.R. Landrum 2654* (MBM); between Palmeiras and Lajes, 2 Dec. 1956, *L.B. Smith & R.M. Klein 8111* (R, NY); 17 km NW from Bocaina do Sul, 11 Feb. 1957, *L.B. Smith & R.M. Klein 11262* (R, UPCB); Ponte Alta, 24 Oct. 1962, *R. Reitz & R.M. Klein 13329* (UPCB); Porto União, Antônio Cândido, 3 Nov. 2001, *Beatriz 3* (MBM); 14 Nov.

1931, *Gurgel s.n.* (R 94131); 14 Nov. 1931, *Gurgel 16235* (RB); São José, Serra da Boa Vista, 24 Oct. 1957, *R. Reitz & R.M. Klein 5391* (K); Videira, Parque da Uva, 26 Oct. 1964, *L.B. Smith & R.M. Klein 12969* (NY, R); no location indicated, Reserva Floresta dos Pilões, 1 Dec. 1950, *A.P. Duarte & J. Falcão 3201* (GUA, RB); W of Serra do Itajaí, Nov. 1876, *F. Muller 195* (R). **São Paulo:** Apiaí, Pinhalzinho-Apiaí, 11 km from Bom Sucesso do Itararé, 13 Dec. 1997, *J.M. Torezan et al. 600* (ESA (2), IAC, UEC); Assis, Estação Ecológica de Assis, 13 Jan. 1993, *G. Durigan 30611* (UEC); Bofete, between Bofete and Guareí, Cachoeira Farm, 25 Jan. 1945, *M. Kuhlmann 1298* (SP, UPCB); Santa Terezinha (Eucatex) Farm, 12 July 2004, *R.A.G. Viani et al. 486* (ESA); Bom Sucesso do Itararé, road from Bom Sucesso do Itararé, 2 km before Mineração São Judas, 15 Dec. 1997, *S.I. Elias et al. 162* (ESA, IAC, UEC); Botucatu, EUCATEX Florestal S.A., Morrinhos Farm, *J.E. Albuquerque et al. 1854* (ESA); Capão Bonito, Barra Mansa Farm, Oct. 1996, *K.D. Barreto et al. s.n.* (ESA 87070); Itararé, Ibiti Farm, Road Itararé-Bom Sucesso do Itararé, 12 Feb. 1995, *P.H. Miyagi et al. 353* (IAC, SPF); 17 km from Itararé to Bom Sucesso do Itararé, 13 Nov. 2003, *J. Paula-Souza et al. 3702* (ESA); Ibiti Farm, Itararé-Bom Sucesso Road, 30 Oct. 1993, *V.C. Souza 4534* (ESA, RB, SPF); Ibiti Farm, 18 Feb. 1993, *V.C. Souza et al. 2358* (ESA, MBM, SPF); Ibiti Farm, 6 Sep. 1993, *V.C. Souza et al. 4322* (ESA, SPF); Itu, Dec. 1825, *L. Riedel s.n.* (NY); near Porto Feliz, Nov. 1825, *L. Riedel 120* (NY (2)); São Paulo, Santo Amaro, 23 Nov. 1913, *A.C. Brade 7482* (SP); 22 Nov. 1934, *A.C. Erns 5* (SP); Sengés, PISA-Papel e Celulose Farm, 18 Dec. 1997, *F. Chung et al. 218* (ESA (2), IAC, UEC); PISA-Papel e Celulose Farm, Poço do Encanto, 18 Dec. 1997, *S.I. Elias et al. 303* (ESA, IAC, UEC); no location indicated, near São Paulo, *K.F.P. von Martius s.n.* (M 90854). No location indicated, Chácara da Associação dos Professores, June 2000, *G.C.T. Ceccantini* (SPF); Fea, Pomar, 22 Nov. 1972, *N. Imaguirre 3138* (RFA); Rio Pardo, 1824, *L. Riedel s.n.* (NY); *F. Sellow s.n.* (G 16302); *F. Sellow 14970* (K); between Paraná and Santa Catarina, *SP 185* (RB); *E.H.G. Ule 1093* (M); collection without indication of collector *120* (NY). **Paraguay. Cannandiyú:** 46 km S from Katuaté, 3 km N from Río Itambery, route Pto. Stroessner, Saltos del Guairá, 18 Dec. 1982, *A. Schinini 23206* (G) (according to Bidá 1995).

Acknowledgments

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List of accepted species of *Symplocos* Jacq. section *Neosymplocos* Brand

1. *Symplocos altissima* Brand
2. *Symplocos angulata* Brand
3. *Symplocos corymboclados* Brand
4. *Symplocos falcata* Brand
5. *Symplocos glandulosomarginata* Hoehne
6. *Symplocos glaziovii* Brand
7. *Symplocos insolita* Aranha, P.W. Fritsch, and Almeda
8. *Symplocos microstyla* Aranha, P.W. Fritsch, and Almeda
9. *Symplocos nitidiflora* Brand
10. *Symplocos organensis* Brand
11. *Symplocos tenuifolia* Brand

Appendix 1

Index to specimens examined. Numbers in parentheses correspond to those of each species in the taxonomic treatment. Collectors whose names were illegible are marked with (*), collections without indication of collector with (**), and collections taken from Bidá (1995) with (***).

Albuquerque, J.E. 1854 (11); Almeda, F. 8782 (4); 8788 (4); 8790 (4); 8792 (10); 8798 (10); 8878 (8); 8910 (7); Altamiro et al. 51 (4); Andrade, A.G., 152 (10); Andrade, N. de s.n. (9); Aranha Filho, J.L.M. 29 (4); 43 (4); Arzolla, F.A.R.D.P. 425 (4).

Baitello, J.B. 594 (4); Barbosa, E. 197 (5); 240 (3); 376 (3); Barreto, K.D. s.n. (11); 2696 (11); Barros, D. de 1051 (9); Beatriz 3 (11); Bertani, D.F. 1 (4); Biank, A.E. 24 (11); Bidá, A. 636 (9); 650 (9); 677 (11); 678 (11); Brade, A.C. 5802 (11); 7482 (11); 14050 (4); 16932 (4).

Campos Porto, P. 831 (3), (4); 2936 (9); Capranica, M.V. s.n. (5); Cardoso, C.M.V. s.n. (11); Carmello-Guerreiro, S.M. 13 (4); Carvalho, P. 84 (11); 96 (11); 171 (11); Carvalho, J.P.M. s.n. (4); Cavalheiro, A.L. s.n. (11); s.n. (11); Ceccantini, G.C.T. 1494 (11); Cervi, A.C. 2990 (11); 3008 (11); 3117 (9); 3279 (11); 3587 (11); 4149 (11); 6101 (5); 6272 (11); Chung, F. 218 (11); Claussen, P. 200 (2); Colli, S. s.n. (11); Collares, J.E.R. 48 (4); 64 (4); Cordeiro, J. 411(11); 921 (5); 1388 (3); 1777 (3); 1512 (5); Custódio Filho, A. 2801 (9).

Dala Rosa, S. 56 (5); 106 (3); Doria, O.V. 39 (11); Duarte, A.P. 3201 (11); 8668 (4); Ducke, A. s.n. (4); Dunaiski, A. 303 (11); Durigan, G. 30611 (11); Dusen, P.K.H. s.n. (4); s.n. (11); 29 (3); 301 (3); 573 (4); 2023 (3); 2135 (4); 3436 (11); 6897 (11); 7152 (11); 7745 (11); 9691 (11); 10331 (11); 11463 (11); 12143 (5); 12195 (5); 13001 (9); 14240 (4); 14512 (11); 15801 (11); 15858 (11).

Edmund., A.A. 51 (4); Edwall, G. s.n. (5); Elias, S.I. 162 (11); 303 (11); Emmerich, M. 138 (10); Erns, A.C. 5 (11).

Farney, C. 1439 (4); Fernandes, H.M. 35 (3); Ferretti, A.R. 140 (4); Filipaki, S.A. s.n. (11); França, G.S. 125 (4); 158 (4); 211 (4); Francisco, E.M. s.n. (11); Freitas, L. 299 (4); Fritsch, P.W. 1803 (11); 1807 (3); 1808 (5); 1809 (5); 1813 (11); 1822 (11); 1823 (9); 1826 (5); 1831 (3); 1832 (5).

Gerht, A. s.n. (4); Gibbs, P.E., 5635 (9); Glaziou, A.F.M. illegible number (1); s.n. (4); 3641 (10); 5888 (4); 6023 (10); 6695 (4); 7769 (4); 11167 (4); 13469 (6); 15189 (2); 15202 (8); 15203 (4); 17130 (10); 17473 (4); 17636 (4); 17696 (4); 18347 (9); 18359 (3); 19618 (1); 20212 (4); Goldenberg, R. 521 (9); 617 (9); 669 (9); Gurgel s.n. (11); s.n. (11); 14648 (11); 16235 (11).

Handro, O. s.n. (5); s.n. (9); Hatschbach, G. s.n. (3); s.n. (3); s.n. (5); s.n. (9); s.n. (11); 82 (11); 1085 (9); 1611 (11); 2690 (11); 6405 (3); 10719 (11); 13053 (5); 13112 (5); 15089 (5); 16838 (3); 17316 (3); 17691 (11); 17760 (11); 17941 (11); 19951 (3); 20737 (11); 22230 (3); 22851 (5); 26859 (5); 27614 (11); 27669 (3); 30669 (11); 30714 (11); 30808 (11); 34895 (5); 35784 (3); 39177 (5); 39198 (11); 39726 (11); 39767 (5); 39788 (11); 40298 (11); 40722 (11); 41840 (11); 43002 (5); 43348 (11); 44366 (11); 45713 (5); 45289 (9); 45741 (11); 46053 (5); 48990 (9); 50102 (5); 50814 (11); 55522 (4); 58185 (11); 67499 (11); 68818 (5); Hemmendorff, E. 3241 (4); Hoehne, F.C.; s.n. (4); s.n. (9); s.n. (9); s.n. (11); 311 (4); 28275 (9).

Imaguirre, N. 2775 (11); 3138 (11); Ivanauskas, N.M. 5068 (5); 5069 (4).

Joly, A.B. CFSC 3685 (7); CFSC 3687 (7); Jönsson, I.G. 4 (11); 132 (11).

Kawasaki, M.L. 571 (4); 1252 (4); Kinoshita, L.S. 16544 (4); Kinupp, V.F. 104 (11); 257 (11); Kirizawa, M. 2568 (4); Koczicki, C. 77 (11); 85 (5); Krapovickas, A. 40910 (11); Krieger, P.L. 11387 (11); Kuhlmann, J.G. s.n. (4); s.n. (4); s.n. (4); s.n. (4); s.n. (11); Kuhlmann, M. s.n. (4); 1298 (11); 1777 (9); 2048 (4); 2531 (4); Kummrow, R. 1730 (11); 2033 (3); 2507 (5); Kuniyoshi, Y.S. s.n. (11); 4077 (5); 4717 (11).

Lacerda, A. 100 (11); 192 (11); 275 (5); Landrum, L.R. 2244 (11); 2430 (11); 2654 (11); 3928 (11); Leitão Filho, H. de F. 1586 (11); 10670 (4); Leite, E.C. 562 (5); Leoni, L.S. 2759 (4); 3076 (4); Liebsch, D. s.n. (11); Lima, H.C. de 5988 (4); 6019 (4); Lima dos Santos, J. 277 (3); Lindberg, G.A. 506 (11); Lindeman, J.C. 1090 (11); 1096 (11); 1874 (11); 1910 (11); 4748 (11); 4917 (11); 5017 (3); Lobão, A.Q. 667 (3); Lombardi, J.A. 939 (4); Loughn, G. s.n. (11).

Macedo, J.H.P. de s.n. (5); Maia, D.C. s.n. (11); Martinelli, G. 11819 (9); 13155 (3); Martius, K.F.P. s.n. (11); Mattos, A. 2011 (11); 14362 (4); 14469 (4); Mazine, F.F. 202 (4); Messias 48 (4); Mgf. 10403 (4); Mielke, C.G. s.n. (11); Miyagi, P.H. 353 (11); Mocochinski, A.Y. 86 (3); 232 (5); Moreira, A.X. 46 (4); Mosen, C.W.H. 619 (11); 4533 (11); Mota, R.C. 1898 (7); Motta, J.T 3017 (5); Muller, F. 195 (11); Muniz, J.R.S. 3 (11).

Negrelle, R.R.B. s.n. (11); 28 (11); 610 (11); A762 (11); Neto, L. 290 (9); Nicolak, V. 110 (11); Nunes, P. s.n. (11).

Occhioni, P. s.n. (11); 5266 (11); 5338 (11); 5342 (5); 5371 (11); 6240 (4); 6255 (4); 7094 (4); 7100 (4); 7830 (4); 8009 (4); 8024 (4); 8702 (4); Oliveira, P.I. 154 (11); 180 (11); 780 (11).

Pabst, G.J.F. 6712 (11); Paula-Souza, J. 2109 (4); 3702 (11); Pereira, E. 6886 (11); 8121 (11); Pessoa, S.V.A., 281 (9); Pirani, J.R. 4896 (4); Plowman, T. s.n. (5); 12823 (4); Poliquesi, C.B. 31 (11); 163 (11); Possette, R.F.S. 265 (11).

Raristyak, L. 105 (9); Reginatto, M. 177 (5); Regnell, A.F. II40 (11); II40ç (11); Reis, J. s.n. (4); Reitz, R. s.n. (11); 1130 (5); 3216 (11); 4130 (5); 5391 (11); 5444 (11); 5830 (11); 6132 (3); 13329 (11); 17849 (11); Ribas, O.S. 412 (11); 1205 (11); 1716 (11); 2185 (3); 2880 (3); 3024 (11); 3961 (11); 4421 (5); 5249 (3); 5760 (3); 5848 (3); 5871 (5); 5888 (11); Riedel, L. s.n. (11); s.n. (11); 120 (11); Robin, M. de J. s.n. (4); 212 (4); 8398 (4); Roderjan, C.V. 273 (11); 1018 (3); 930 (3); Rolian, C.B. 7472 (11); Rotta, E. s.n. (11); Rubens, A.A.B. 198 (4); 255 (4); 264 (4).

Salimon, C.I. s.n. (11); Santos, E.P. 284 (3); 348 (3); Scheer, M. 451 (3); Seele, C. 1055 (4); Sellow, F. s.n. (11); 221 (9); 4806 (11); 14970 (11); Shepherd, G.J. 6137 (11); 12859 (4); Silva, J.M. 1053 (3); 1696 (3); 2055 (3); 2120 (5); 2622 (5); Smith, L.B. 7392 (5); 7557 (5); 8111 (11); 8495 (11); 11262 (11); 12969 (11); Souza, V.C. 2358 (11); 4322 (11); 4534 (11); 12147 (4); 23397 (4); SP 185; (11); Stange, E.J. 6 (3); Stehmann, J.R. 3001 (4).

Takeda 904 (11); Talbot, H.F. s.n. (9); Tiepolo, G. 13 (5); 47 (5); 48 (11); 564 (5); 600 (11);

Torezan, J.M. 600 (11).

Uhlmann, A. s.n. (11); Ule, E.H.G. 644 (4); 2475 (2); 1093 (11); Ururahy, J.C.C. 21 (4).

Vasconcellos, M.F. de s.n. (8); Viani, R.A.G. 486 (11); Vicentini, A. 168 (11).

Wesenberg, J. 628 (4); Widgren, J.F. 370 (11); 1157½ (11).

Ziller, S.R. 615 (11); 713 (11); 810 (11); 1526 (11); 1942 (11).

* 5792 (5).

** 120 (11).

*** Schinini, A. 23206 (11).

Appendix 2

Comparison of Brand (1901) and Bidá's (1995) treatment of *Symplocos* section *Neosymplocos* to that in the present work. Synonyms are indented. Specimens of taxa marked with an asterisk were not available at the time of Brand's revision.

Brand 1901	Bidá 1995	Present treatment
S. aegrota	S. aegrota	S. falcata
S. altissima	S. altissima	S. altissima
S. angulata	S. angulata	S. angulata
		S. insolita*
S. ascendens	S. falcata	S. falcata
S. corymboclados	S. corymboclados	S. corymboclados
	S. hatschbachii*, *nom. ined.*	S. hatschbachii*, *nom. ined.*
S. densiflora var. densiflora	S. densiflora	S. falcata
S. densiflora var. minor	S. densiflora var. minor	S. falcata
S. falcata	S. falcata	S. falcata
	S. ascendens	S. ascendens
		S. aegrota
		S. densiflora var. densiflora
		S. densiflora var. minor
S. glaziovii	S. glaziovii	S. glaziovii
S. nitidiflora	S. nitidiflora	S. nitidiflora
S. organensis	S. organensis	S. organensis
		S. microstyla
S. tenuifolia	S. tenuifolia	S. tenuifolia
	S. reitzii, *nom. ined.*	S. reitzii, *nom. ined.*
	S. glandulosomarginata	S. glandulosomarginata
Totals:		
11 species, 12 taxa	13 species	11 species

Appendix 3

Index to scientific names. Synonyms are italicized.

Barberina, section 408
Bobua, section 428
Epigenia, subgenus 408
Eusymplocos, subgenus 408
Ericales, order 407
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Microsymplocos, subgenus 408, 410
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Symplocaceae, family 407, 408
Symplocastrum, section 410
Symplocos
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S. altissima 411, 414, 415
S. angulata 415–417
S. ascendens 420
S. candelabrum 428
S. ciponimoides 408
S. corymboclados 409, 416, 417, 419
S. corymboclados var. *micromorpha* 417
S. densiflora 421
S. densiflora var. *minor* 421
S. falcata 409, 420, 422, 423
S. glandulosomarginata 409, 411, 425, 426
S. glaziovii 411, 427, 429
S. insolita 411, 428, 431
S. lanata 408
S. micrantha 408
S. microstyla 416, 430, 432
S. nitidiflora 409, 433–435
S. organensis 409, 434, 436, 437
S. tenuifolia 436, 439
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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES
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Rediscovery and Phylogenetic Placement of *Philcoxia minensis* (Plantaginaceae), with a Test of Carnivory

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The recently described genus *Philcoxia* comprises three rare species endemic to seasonally dry areas of deep white sand among cerrado vegetation in Brazil. One of these, *P. minensis*, was described from a single fragmentary specimen collected in the Serra do Cabral in Minas Gerais, Brazil, the detailed locality of which was unspecified. We report the rediscovery of *P. minensis* in this mountain range and provide an augmented description, detailed illustrations, and locality and habitat information. On the basis of morphology, *Philcoxia* has been considered to be a member of either the tribe Scrophularieae or tribe Gratioleae, in the latter case close to *Gratiola* or members of the informally named subtribe "Dopatriinae." We tested the classification of *Philcoxia* with a phylogenetic analysis of *P. minensis* and other samples of Gratioleae based on molecular sequence data from the internal transcribed spacer region of nuclear DNA and *rbcL*, 3′-*ndhF*, *matK*/3′-*trnK*, and *trnL*-*trnF* regions of chloroplast DNA. Results demonstrate solid support for the inclusion of *P. minensis* within the Gratioleae, but relatively distant from both *Gratiola* and "Dopatriinae." Instead, it forms the second-divergent lineage among the samples tested in separate and combined-gene analyses. Previous workers have noted that the peltate leaves with stalked capitate glands on the upper surface and what they considered to be circinnate vernation in *Philcoxia* are similar to those found in some carnivorous plant families. Our additional observation of nematode worms on the surfaces of most leaves of all species of *Philcoxia* prompted us to conduct a test of carnivory in *P. minensis*. Negative results for protease activity suggest that *Philcoxia* is not carnivorous. Because of various potential sources of error, however, the possibility of carnivory in *Philcoxia* should not be entirely ruled out.

The recently described genus *Philcoxia* P. Taylor and V.C. Souza consists of three rare species endemic to Brazil (Taylor et al. 2000). The genus is characterized by subterranean stems, orbicular to reniform usually peltate leaves situated on or below the soil surface, flowers on a leafless scape, a deeply 5-lobed calyx with subequal lobes, two adaxial and included stamens, monothecous glabrous anthers that are oriented transversely to the filament, lack of staminodes, and a 4-valved capsule. The peltate leaves and unusual subterranean stems of *Philcoxia* are extraordinary features within Plantaginaceae (*sensu* Angiosperm Phylogeny Group 2003; Taylor et al. 2000). All species occur in areas of white sand surrounded by cerrado vegetation between 800 and 1450 m ele-

vation. Each of the species is named for the state of Brazil to which it is endemic: *P. bahiensis* V.C. Souza and Harley, *P. goiasensis* P. Taylor, and *P. minensis* V.C. Souza and Giulietti.

The last of these was until now only documented from the type, collected in the Serra do Cabral in 1981 with the precise locality not indicated. Some of the authors who described the genus conducted a field trip to the Serra do Cabral but could not relocate *Philcoxia minensis* (Taylor et al. 2000). During a field trip to the Serra do Cabral in October 2001 to study Melastomataceae and members of Ericales, the first three authors of the present paper by chance encountered *P. minensis* growing in a flat undisturbed area of very dry deep white sand among cerrado vegetation. The presence of *Discocactus placentiformis* (Lehm.) K. Schum. in the immediate vicinity indicated the well drained habitat in which *P. minensis* occurs.

The presumably highly specialized vegetative characters of *Philcoxia* have obscured the relationships of this genus to other members of Scrophulariaceae *sensu lato*. Souza (1996) placed it in tribe Scrophularieae *sensu* Thieret (1967) on the basis of the shared features of its posterior corolla lobes overlapping the lateral lobes and monotelic (cymose) inflorescence. In contrast, Taylor et al. (2000), in interpreting the inflorescence as polytelic (racemose) and citing a general, although unspecified, resemblance, suggested affinity with *Gratiola* L. and *Dopatrium* Buch.-Ham. ex Benth., predominantly aquatic genera in the tribe Gratioleae *sensu* Wettstein (1891). Fischer (2004) placed *Philcoxia* within an informally recognized subtribe "Dopatriinae" of tribe Gratioleae also containing the mostly aquatic genera *Deinostema* Yamazaki, *Dopatrium*, *Hydrotriche* Zucc., and *Limnophila* R. Br.

In their original paper describing *Philcoxia*, Taylor et al. (2000) noted the general convergent similarity to members of Lentibulariaceae, especially in the peltate leaves with reportedly circinnate vernation and abundant stalked capitate glands on the adaxial surfaces. They stated that field observations did not support the view that the glands had any insectivorous function, although the detailed basis for this conclusion was not mentioned. One piece of evidence for carnivory would be the presence of dead organisms on the leaf surfaces. We carefully examined all leaf surfaces from both our recent collections and the isotypes of the other two species, and did not observe any insects. Upon magnification to 60×, however, sparse to rather dense brown threads on the upper surfaces on most of the upper leaf surfaces of each species were apparent (Fig. 1A). Increasing the magnification to 1000× confirmed that these were nematode worms (Fig. 2). The leafless scapose inflorescence and open, nutrient-poor, fire-prone habitat in which *Philcoxia* species occur are consistent with the form and habitat of many carnivorous plants (Lloyd 1942; Givnish 1989). The habitat of white sand

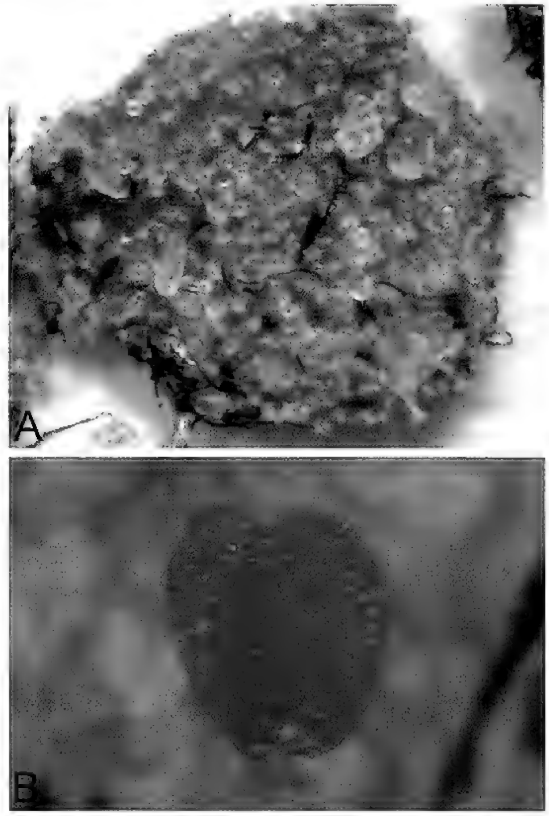


FIGURE 1. Leaf blades of *Philcoxia*. A. Nematode worms (the dark threads) attached to the upper surface of a leaf blade of *Philcoxia goiasensis*. All *Philcoxia* species exhibit leaves with such nematodes. B. Living leaf blade of *P. minensis*. B photo, J. L. M. Aranha Filho.

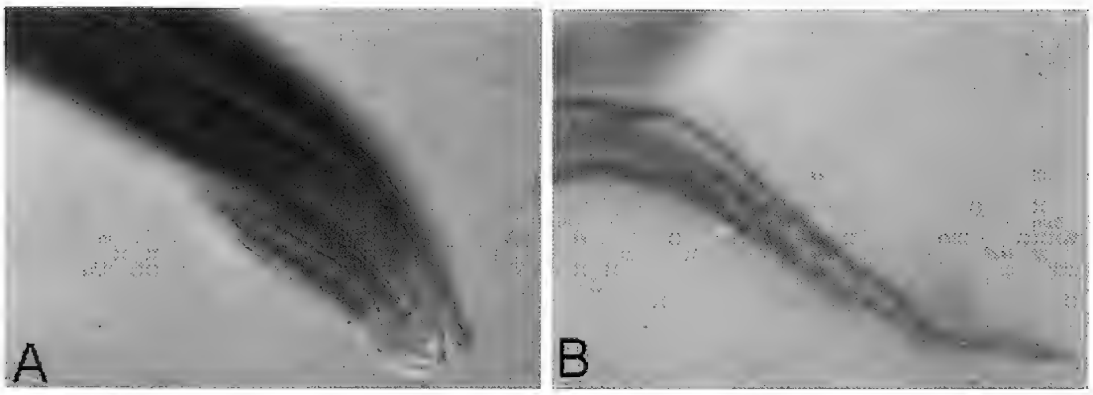


FIGURE 2. High magnification (1000x) of nematode worm found on the leaves of *Philcoxia minensis* showing head (A) and tail (B).

resembles particularly that of *Genlisea* Benth. and Hook. f. (Lentibulariaceae) in Brazil, a genus that traps and digests ciliate protozoa (Barthlott et al. 1998). We therefore hypothesized that *Philcoxia* was carnivorous in the broad sense, using nematodes and possibly other soil organisms as a source of nutrition.

Here we report the rediscovery of *Philcoxia minensis* in Serra do Cabral and provide an augmented description, detailed illustrations, and locality and habitat information for the species. We also infer the phylogenetic placement of *Philcoxia* using DNA sequence data from the internal transcribed spacer region of nuclear ribosomal DNA (ITS), and the *trnL-trnF* intergenic spacer, the *rbcL* gene, the 3′ end of the *ndhF* gene, and the *matK* gene/3′-*trnK* intron of chloroplast DNA with analyses that comprise both newly published sequence data from other members of Gratioleae and sequences from GenBank. Finally, we tested the hypothesis of carnivory in *Philcoxia* by conducting a simple test for protease activity in *P. minensis* with live field-collected plants from the Serra do Cabral.

MATERIALS AND METHODS

TAXONOMIC TREATMENT.—The description of *Philcoxia minensis* is based on field observations and collections made in October 2001 and September and October 2005 by the first three authors. Collected material consists of dried herbarium specimens and flowering and fruiting plants preserved in 95% ethanol.

PHYLOGENETICS.—Taxa of the tribes Scrophularieae and Gratioleae, the two groups considered likely to contain the closest relatives of *Philcoxia*, form two rather distantly related clades within Lamiales in analyses based on DNA sequence data, with other members of the former Scrophulariaceae interspersed among various clades of Lamiales (Olmstead et al. 2001; Bremer et al. 2002; Rahmanzadeh et al. 2004; Albach et al. 2005; Oxelman et al. 2005). We therefore assessed the general placement of *Philcoxia* among the Lamiales by constructing a data set that included one or more representatives of most well supported major clades of Lamiales recovered in the global analyses of Bremer et al. (2002). Sequence data from the chloroplast gene *rbcL*, chloroplast intergenic spacer region *trnL-trnF*, and the 5.8S region of nrDNA were employed for this analysis because taxa of Lamiales representative of the major clades have been sequenced for these three genic regions and are available from GenBank (Table 1). We particularly emphasized sampling taxa that have been placed in the tribes Gratioleae and Scrophularieae (*sensu* Fischer 2004). On occasion, different species in the same genus were sequenced for different genic regions and combined into a single terminal (Table 1). Because the combined terminals only occurred in clades that have

TABLE 1. GenBank accession numbers of taxa of Lamiales *trnL-trnF*, *rbcL*, and nuclear ribosomal 5.8S sequences used in this study. Herbarium voucher information is provided for the newly reported nr 5.8S sequence of *Angelonia*.

Taxon	*trnL-trnF*	*rbcL*	nr 5.8S
Acanthaceae: *Ruellia*	AF482604	L12595	AY530731
Bignoniaceae: *Jacaranda*	AJ430914	AF102647	—
Byblidaceae: *Byblis*	AF482605	L01891	—
Calceolariaceae: *Calceolaria*	AJ60861	AF123669	AJ579467
Gesneriaceae: *Columnea*	AF482612	AF170228	AF543251
Lamiaceae: *Lamium*	AJ608588	Z37403	AY443449
Lentibulariaceae: *Pinguicula*	AF482619	L01942	AB198348
Martyniaceae: *Proboscidea*	AJ608573	L01946	AY178642
Oleaceae: *Olea*	AF231867	AJ001766	AJ585193
Orobanchaceae: *Melampyrum*	AF482608	AF026834	—
Pedaliaceae: *Sesamum*	AF479010	L14408	AF478946
Pedaliaceae: *Uncarina*	AF482610	—	AY178650
Plantaginaceae: *Angelonia pratensis* Gardn. ex Benth.; *Almeda et al. 8960*, CAS, UEC)	AJ608618	AF123672	EU074164
Plantaginaceae: *Capraria*	AJ608608	—	—
Plantaginaceae: *Galvezia*	AY492177	—	AY492104
Plantaginaceae: *Lindenbergia*	AJ608586	AF123664	—
Plantaginaceae: *Melosperma*	AY492185	—	AY492112
Plantaginaceae: *Monttea*	AY492187	—	AY492114
Plantaginaceae: *Ourisia*	AY492189	—	AY492116
Plantaginaceae: *Plantago*	AY101952	L36454	AJ548984
Plantaginaceae: *Stemodiopsis*	AJ608565	—	—
Plantaginaceae: *Veronica*	AF513338	L36453	AY540868
Plocospermataceae: *Plocosperma*	AJ430903	Z68829	—
Schlegeliaceae: *Schlegelia*	AJ43093	L36448	—
Scrophulariaceae: *Diascia*	AJ608595	—	AJ616319
Scrophulariaceae: *Limosella*	AJ608587	—	AJ550588
Scrophulariaceae: *Myoporum*	AJ430934	L36445	—
Scrophulariaceae: *Nemesia*	AF380874	AF123663	AJ616325
Stilbaceae: *Stilbe*	AJ608629	Z68827	AJ616331
Tetrachondraceae: *Tetrachondra*	AJ430939	AF254787	—
Verbenaceae: *Verbena*	AF231885	Z37473	AF47779

previously been demonstrated to have strong statistical support, we assume that the use of such combinations did not affect the placement of *Philcoxia*. Based on the results of Bremer et al. (2002), we used *Plocosperma* (Plocospermataceae) as outgroup for the rest of Lamiales. Thirty-five terminals were included in this analysis.

After the general placement of *Philcoxia* was assessed, a second main data set was constructed to more specifically address the placement of *Philcoxia* among an expanded set of other species of "core" Gratioleae (Table 2). The genic regions employed for the analysis were ITS (including the ITS 1 and ITS 2 spacers and the 5.8S region), *trnL-trnF*, *rbcL*, *matK*/3′-*trnK*, and 3′-*ndhF*. These five regions were employed because of their demonstrated utility in resolving relationships of other groups within the former Scrophulariaceae (Olmstead et al. 2001; Rahmanzadeh et al. 2004; Albach et al. 2005; Oxelman et al. 2005) and the extensive number of GenBank sequences available for

TABLE 2. GenBank accession numbers of core Gratioleae ITS, *trnL-trnF*, 3′-*ndhF*, *rbcL*, and *matK*/3′-*trnK* sequences used in this study. Asterisks indicate newly reported sequences. Plus signs indicate that the taxon with the sign and the one below it have been combined into a single terminal in the analysis. Table cells with horizontal lines have no sequence data. Voucher and locality information is provided for newly reported sequences, with herbarium acronym in parentheses. CAS = California Academy of Sciences; UEC = Universidade Estadual de Campinas.

Taxon	Collection #	Locality	ITS	*trnL-trnF*	3′-*ndhF*	*rbcL*	*matK*/3′-*trnK*
Achetaria scutellarioides Wettst.	*D. Estes*		—	—	EF527469	—	—
Amphianthus pusillus Torr.			—	—	AF123674	AF123673	—
Bacopa eisenii (Kellogg) Pennell	*Fritsch & Cruz 1789* (CAS)	Butte Co., California, U.S.A.	EF467894*	EF467888*	EF467911*	EF467906*	EF467900*
Bacopa monnieri (L.) Pennell			AY492095	AY492170	EF527447	—	AY667458
Bacopa repens (Sw.) Wettst.	*Fritsch & Cruz 1788* (CAS)	Butte Co., California, U.S.A.	EF467893*	EF467887*	EF467910*	EF467905*	EF467899*
Dopatrium junceum (Roxb.) Buch.-Ham.	*Fritsch & Cruz 1787* (CAS)	Butte Co., California, U.S.A.	EF467891*	EF467885*	EF467908*	EF467903*	EF467897*
Gratiola neglecta Torr.[1]			—	AJ608591	AF188183	AF026827	—
Hydrotriche hottoniiflora Zucc.	*Fritsch 1791* (CAS)	Cultivated, Univ. of Wisconsin, U.S.A.	EF467892*	EF467886*	EF467909*	EF467904*	EF467898*
Leucospora multifida Nutt.			—	AJ608597	EF527453	—	—
Limnophila × *ludoviciana* Thieret	*Fritsch & Cruz 1790* (CAS)	Butte Co., California, U.S.A	EF467896*	EF467890*	EF467913*	—	EF467902*
Limnophila aromatica (Lam.) Merrill	*D. Estes*		—	—	EF527457	—	—
Mecardonia acuminata (Walter) + Small	*D. Estes*		—	—	EF527449	—	—
Mecardonia procumbens Small			AY492111	AY492184	—	—	AY492152
Otacanthus azureus (Linden) A. Ronse+			—	—	EF527468	—	—
Otacanthus caeruleus Lindl. +			—	—	—	—	AY667459
Otacanthus sp.			AY492115	AY492188	—	—	—
Philcoxia minensis V.C. Souza & Giulietti	*Almeda et al. 8544* (CAS, UEC)	Minas Gerais, Brazil	EF467895*	EF467889*	EF467912*	EF467907*	EF467901*
Scoparia dulcis L.			AY492119	AY492191	EF527450	—	AY492162
Scoparia 'Melongolly Blue'	*D. Estes*		—	—	EF527451	—	—
Scoparia plebeja Cham. & Schltdl.	*D. Estes*		—	—	EF527452	—	—
Sophronanthe pilosa (Michx.) Small	*D. Estes*		—	—	EF527459	—	—
Stemodia durantifolia (L.) Sw.			AY492120	—	—	—	AY492164
Stemodia glabra Spreng.			—	AJ608566	AJ617584	—	—
Stemodia schottii Holz.	*D. Estes*		—	—	EF527470	—	—
Stemodia suffruticosa HBK.	*D. Estes*		—	—	EF527455	—	—
Stemodia verticillata (Mill.) Hassler	*D. Estes*		—	—	EF527454	—	—

[1] As *Gratiola pilosa* in GenBank but probably *G. neglecta* based on comparative sequence data of D. Estes (unpubl. data).

these regions from members of core Gratioleae. Based on the results of Albach et al. (2005) and our Lamiales-wide analysis, we used *Mecardonia* as outgroup. Of the 64 sequences of core Gratioleae used in the study, 30 are here published for the first time, from seven taxa (Table 2). We conducted separate ITS and cpDNA analyses to detect any discordance between nuclear and chloroplast data partitions as determined from an incongruence length difference (ILD) test (Farris et al. 1994), and a combined 5-gene analysis to provide a total-evidence phylogenetic estimate.

Total genomic DNA was extracted from fresh, silica-gel dried, or herbarium leaf samples with DNeasy Plant Mini DNA extraction kits (Qiagen, Inc.). Extraction, PCR amplification, PCR prod-

uct purification, cycle sequencing, and sequence generation followed the protocols in Wang et al. (2004). Sequences were edited with the computer program Sequencher 4.7 (Gene Codes Corp.). All sequences have been deposited in GenBank (Tables 1 and 2). The gene *rbcL* was amplified and sequenced as in Fritsch et al. (2001) with primers from Olmstead et al. (1992), the 3′-*ndhF* region as in Fritsch et al. (2004), as modified from Clausing and Renner (2001), with primers from Olmstead and Sweere (1994), and the ITS, *trnL-trnF*, and *matK*/3′-*trnK* regions as in Wang et al. (2004) with primers from Swensen et al. (1998), Taberlet et al. (1991), and Sang et al. (1997), respectively. Target sequences unsuccessfully amplified with the external primers were often successfully amplified in two fragments with an external and one of the internal primers.

Sequence alignment was manual. The aligned sequence matrices are available from the authors upon request. Phylogenetic analyses employed maximum parsimony (MP) for the analysis of Lamiales, and MP, maximum likelihood (ML), and Bayesian inference (BI) for the placement of *Philcoxia* within core Gratioleae. MP heuristic searches and parsimony bootstrapping (bt; Felsenstein 1985) were conducted with the computer program PAUP* version 4.0b10 (Swofford 2002) by following the procedure of Wang et al. (2004). Gaps were treated as missing data (the default option in PAUP*). The ML analyses were performed with the PAUP* version 4.0b10 for UNIX (Swofford 2002) under the GTR + I + Γ model, in accordance with the recommendations of Huelsenbeck and Rannala (2004). One hundred ML bootstrap replicates were performed on the Gratioleae data set. Four iterations were run, with parameters for the initial iteration estimated from a neighbor-joining tree and those for subsequent iterations estimated from the previous iteration. The BI analysis was conducted with MrBayes version 3.1.2 (Huelsenbeck and Ronquist 2001) by using uniform prior probabilities and estimating base frequencies and the parameters for the GTR + I + Γ model. Four chains of the Markov chain Monte Carlo were run by beginning with a random tree and sampling one tree every 100 generations for 3,000,000 generations. The phylogenetic estimate was based on trees sampled after the first 30,000 generations of the chain, which were used as "burn in" after stationarity was reached. To estimate the posterior probability (pP) of recovered branches, 50% majority-rule consensus trees were created.

Test for carnivory.—The protease test of Hartmeyer (1997) as modified by Meyers-Rice (1999) was performed to check for carnivory in *Philcoxia*. Due to the harsh environmental conditions (i.e., extreme heat, sand blown by wind) in which *Philcoxia* grows, the test could not be performed in the field. Thus, six whole plants were transported in their sand substrate to the laboratory where the test could be conducted more easily. A 10% solution of baker's yeast was pipetted onto the upper surface of the leaves (still attached to the plant) and the leaf was placed between two pieces of Ilford XP2 ASA 400 black and white film with the emulsion side of the film toward the leaf. The film was made flat with a herbarium paper backing that fit each piece of film, and the paper-film-leaf sandwich was clipped together so that the leaf pressed against the film. After 48 hours the film was examined; any clearing of the originally opaque surface would indicate digestion of the gelatin layer of the film and thus protease activity by the plant. All tests were conducted under ambient room conditions in indirect sunlight. Prior to field work in Brazil, a preliminary test was performed in the laboratory on a species of cultivated *Drosera* that produced a vigorous positive reaction. As a result, the reagents and equipment used were brought to Brazil for the test.

Because the leaves of *Philcoxia* were often found covered with sand grains adhering to the glands, care was taken to first remove as many grains as possible with forceps. Two of the plants were tested while remaining in their native soil. Because it was technically difficult to set up the test as such, the other four were tested by placing them in Petri dishes under a moist paper towel under natural indirect light. Some tests were also conducted with leaves clipped from the stems. Pieces of freshly cut pineapple were employed as a positive control. Three types of negative con-

trols were used: film only, film plus yeast extract, and film plus yeast extract on the presumably non-carnivorous plant *Ixora coccinea* L. (Rubiaceae). We performed the same test in the U.S. on *Hydrotriche hottoniiflora* and *Limnophila* × *ludoviciana* plants collected from the same locality as the material used for molecular analysis.

Results

Taxonomic Treatment

Philcoxia minensis V.C. Souza & Giulietti, Kew Bull. 55:161. 2000. Type.— Brazil. Minas Gerais: Joaquim Felício (município), Serra do Cabral, 17 April 1981, *Rossi et al. CFCR 1089* (holotype: SPF not seen). Figures 1B, 3–8.

Terrestrial, probably perennial delicate and wiry herbs 10–26 cm tall. Root unbranched or sparsely branched, knobby, dark orange, not fibrous. Rhizomes horizontal, arising from upright stems or rarely the root, unbranched, 0.5–5 cm long or more, mostly <0.25 cm thick, glabrous; old rhizomes dark orange, stiff-wiry, young rhizomes white, capillary and delicate. Upright stems produced at root apex and along rhizomes, subterranean, swollen or tuber-like, 2–5 mm long. Leaves 5–10, irregularly arranged on upright stems, or frequently borne on young rhizomes, then 1–6 and alternately arranged. Petiolar tissue not clearly differentiated from that of the rhizomes; petioles from upright stems 0.5–3 cm long or more, radiating in all directions, those from young rhizomes 0.1–2 cm long; young laminae conduplicate; lamina subterranean or (when mature) at soil surface, oriented at a ± 90° angle from petiole, green in living stage and when dry, suborbicular to subreniform, subpeltate to peltate, convex-hemispherical adaxially, slightly concave abaxially, 0.5–1.5 × 0.5–1.5 mm, vaguely palmately 3-nerved abaxially with each of two lateral nerves bifurcating distally, adaxially covered with ± sessile and stalked glands with pluricellular heads, abaxially glabrous, base rounded (when peltate) to cordate, margin entire, apex ± emarginate. Inflorescences usually several from each upright stem, aerial except at base, paniculate or occasionally unbranched, zigzag-racemose distally, erect, 10–26 cm long, peduncle green, terete, 0.5 mm thick, glabrous; bracts basifixed, inconspicuous, ± appressed to peduncle or pedicels at least basally, deltoid, 0.5–1.5 × ca. 0.25 mm at base, glabrous, margin entire, apex acute. Flowers often partly to completely resupinate, ebracteolate, unscented. Pedicels green, ascending or upcurved, terete, 1–2.7 cm long at anthesis, minutely glandular-puberulent, more densely so distally just below calyx, trichomes to ca. 0.07 mm long with unicellular stipe and pluricellular head, commonly elongating in fruit. Calyx ± equally 5-lobed; lobes distinct nearly to base, elliptic, 0.7–1 × 0.4–0.6 mm, glabrous or very sparsely glandular-puberulent at base abaxially, erect and persisting after fruits have fallen. Corolla sympetalous, salverform, bilabiate, upper (adaxial) lip (1-) 2-lobed, lower (abaxial) lip 3-lobed, upper lobes covering lower lobes in bud (antirrhinoid aestivation); tube 3–4 mm long, slightly incurved toward the adaxial side, slightly gibbous adaxially at base, lacking a palate at throat, flaring into the lobes, externally glabrous, internally very pale lavender, with a lighter square color pattern at floral orifice, white-clavate-puberulent abaxially, white-pilose adaxially on distal half and densely so just below filaments; lobes (4)5, pale lavender with darker unbranched or dichotomous venation, spreading, ± obovate, 2–3 × 1.75–3 mm, apically undulate, shallowly emarginate, or subtruncate. Stamens 2, adaxial, inserted on corolla ± midway up tube, included in the corolla; filaments straight, flattened, 0.5–0.7 mm long, sparsely puberulent on proximal half and bearing a callose knobby thickening (possibly a rudimentary theca) distally that is disjunct from and just below anther, connective flared toward the theca above the thickening; anthers positioned just below stigma in tube, oriented transverse to filament, dorsifixed, monothecous, dehiscing by a longitudinal

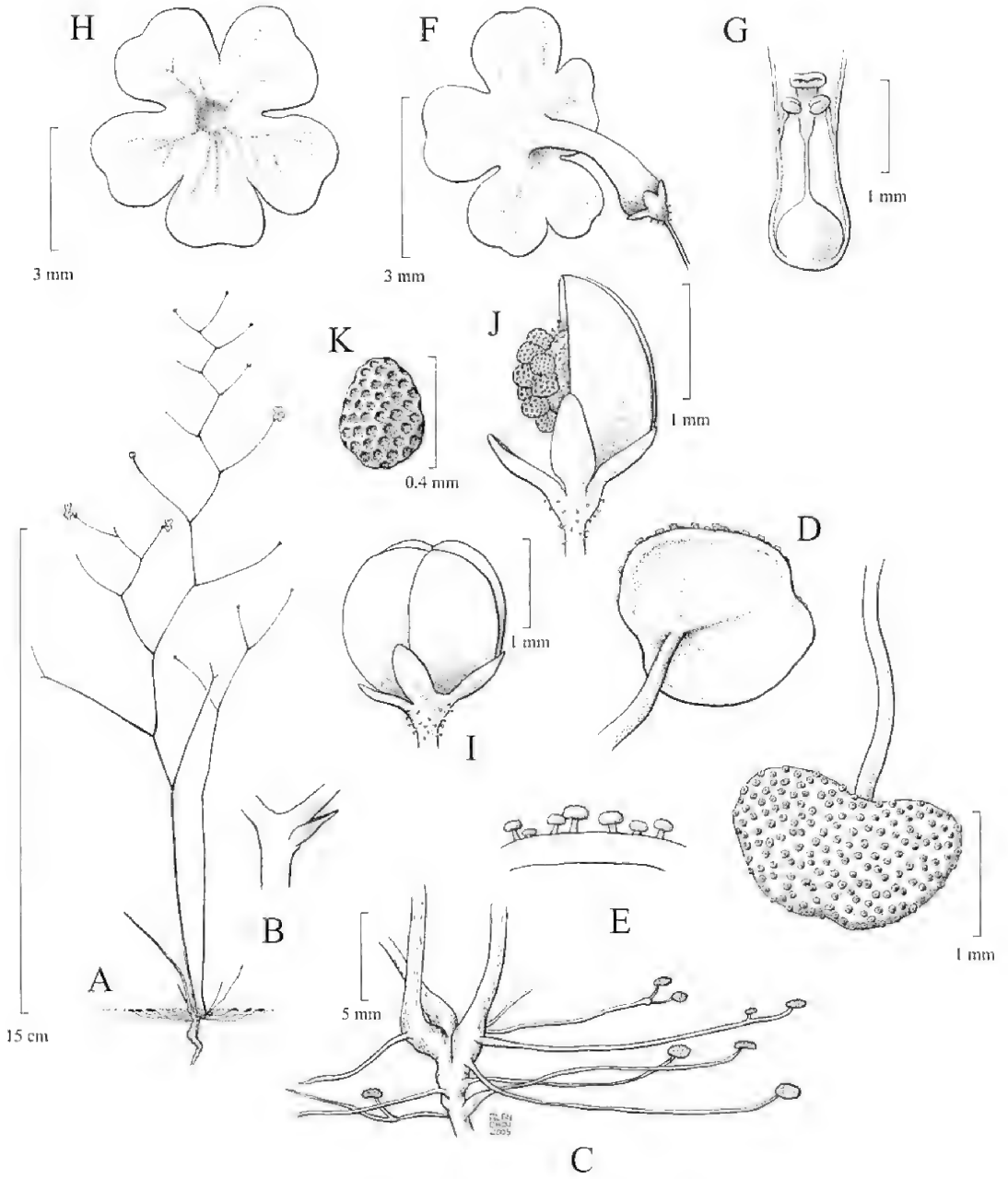


FIGURE 3. *Philcoxia minensis* V. C. Souza & Giulietti. A. Habit showing subterranean root, horizontal rhizomes, leaves, and aerial inflorescence. B. Inflorescence bract. C. Upright stem, rhizomes, leaves, and basal portion of inflorescence. D. Petiole and leaf blade, abaxial (left) and adaxial (right) surface. E. stalked glands on adaxial surface of leaf blade. F. Flower in lateral-rear view. Note gibbous portion at base of corolla tube. G. Corolla tube in longitudinal section showing arrangement of the androecium and gynoecium. H. Corolla, face view. I. Capsule. J. Capsule, half-view exposing the seeds. K. Seed. From *Almeda et al. 8544* (CAS).

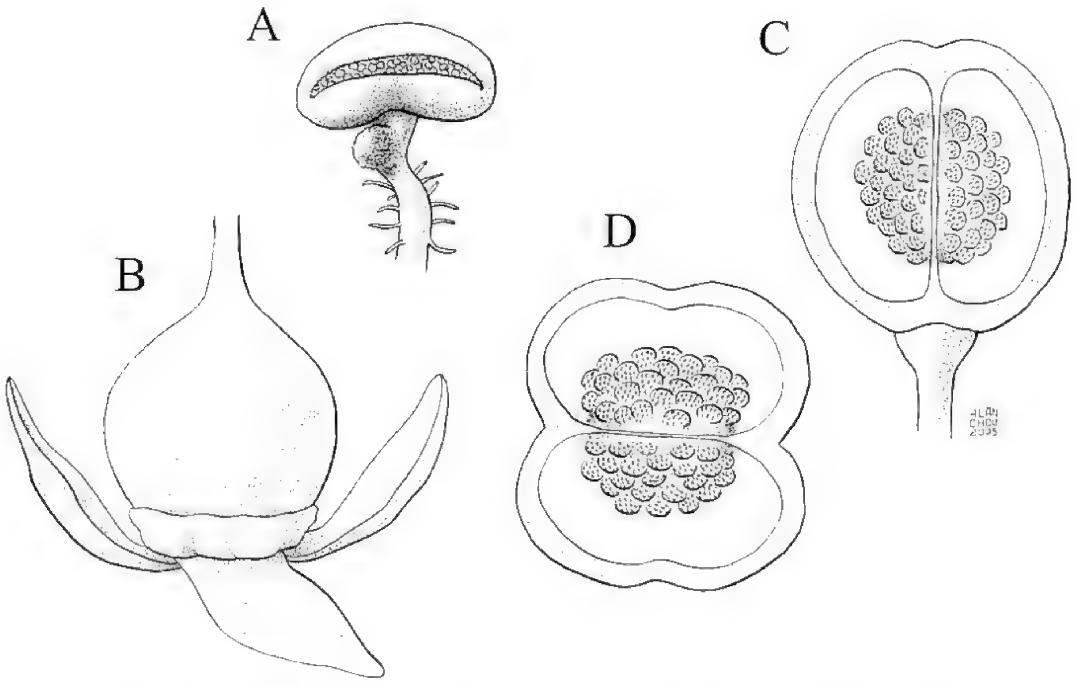


FIGURE 4. *Philcoxia minensis* V. C. Souza & Giulietti. A. Monothecous anther with callose thickening beneath it, the latter possibly a rudimentary theca and the flared portion above it thus part of the connective. B. Calyx and ovary with annular disk at ovary base. C, D. Ovary in longitudinal section (C) and cross-section (D) showing axile placentation and numerous ovules. From *Almeda et al. 8544* (CAS).

slit, ellipsoid or subreniform, 0.5 × 0.5 mm, rounded at the ends, glabrous; staminodia lacking. Gynoecium syncarpous, 2-carpellate; ovary superior, 2-locular, globose or ovoid, 0.7–0.8 mm long, with an annular nectary disk surrounding base; style terminal, solitary, filiform for basal 1–1.5 mm, abruptly expanded and laterally compressed-claviform or obconic for distal 0.8 mm, caducous; stigma positioned just above anthers in floral tube and bent toward abaxial side of corolla, bilabiate; lobes ± appressed to one another, similar in size and shape; ovules borne on two axile placentae, numerous. Fruit a dry capsule 2 × 2 mm, dehiscing septicidally and then loculicidally from apex along 4 valves; capsule valves entire, glabrous. Seeds black, ovoid, 0.4 × 0.25 mm long, estipitate; testa reticulate-foveolate.

ADDITIONAL SPECIMENS EXAMINED.—BRAZIL. **Minas Gerais:** Município Joaquim Felício. Serra do Cabral, 16 km S of Armazém de Laje and 8 km N of Joaquim Felício, 17°42′S, 44°11′W, cerrado vegetation on white sand at 1067 m, 18 Oct 2001, *F. Almeda, A. B. Martins, P. W. Fritsch, and R. Belinello 8544* (BHCB, CAS, MO, UEC, USP); 24 Sep 2004, *F. Almeda, A. B. Martins, and R. Belinello 9137* (CAS, MO, NY, UEC).

PHYLOGENETICS.—MP analysis of the three-gene Lamiales data set resulted in 19 equally parsimonious trees of 1274 steps (CI = 0.47; RI = 0.82; Fig. 9). Although the strict consensus of these trees is highly unresolved, the placement of *Philcoxia* is recovered within a strongly supported clade comprising core Gratioleae (bt = 99), as sister to *Gratiola* (bt = 65). *Mecardonia* forms the first-diverging lineage of the clade (bt = 94).

The MP analysis of the expanded core Gratioleae clade with ITS (12 terminals) resulted in a single optimal tree of 406 steps (CI = 0.67; RI = 0.63; Fig. 10). The strict consensus recovered a clade of *Bacopa* species (bt = 100; pP = 1.00) as the first-diverging lineage (bt = 63; pP = 1.00). In the sister clade to *Bacopa*, the following successive sister lineages were recovered: *Dopatrium* +

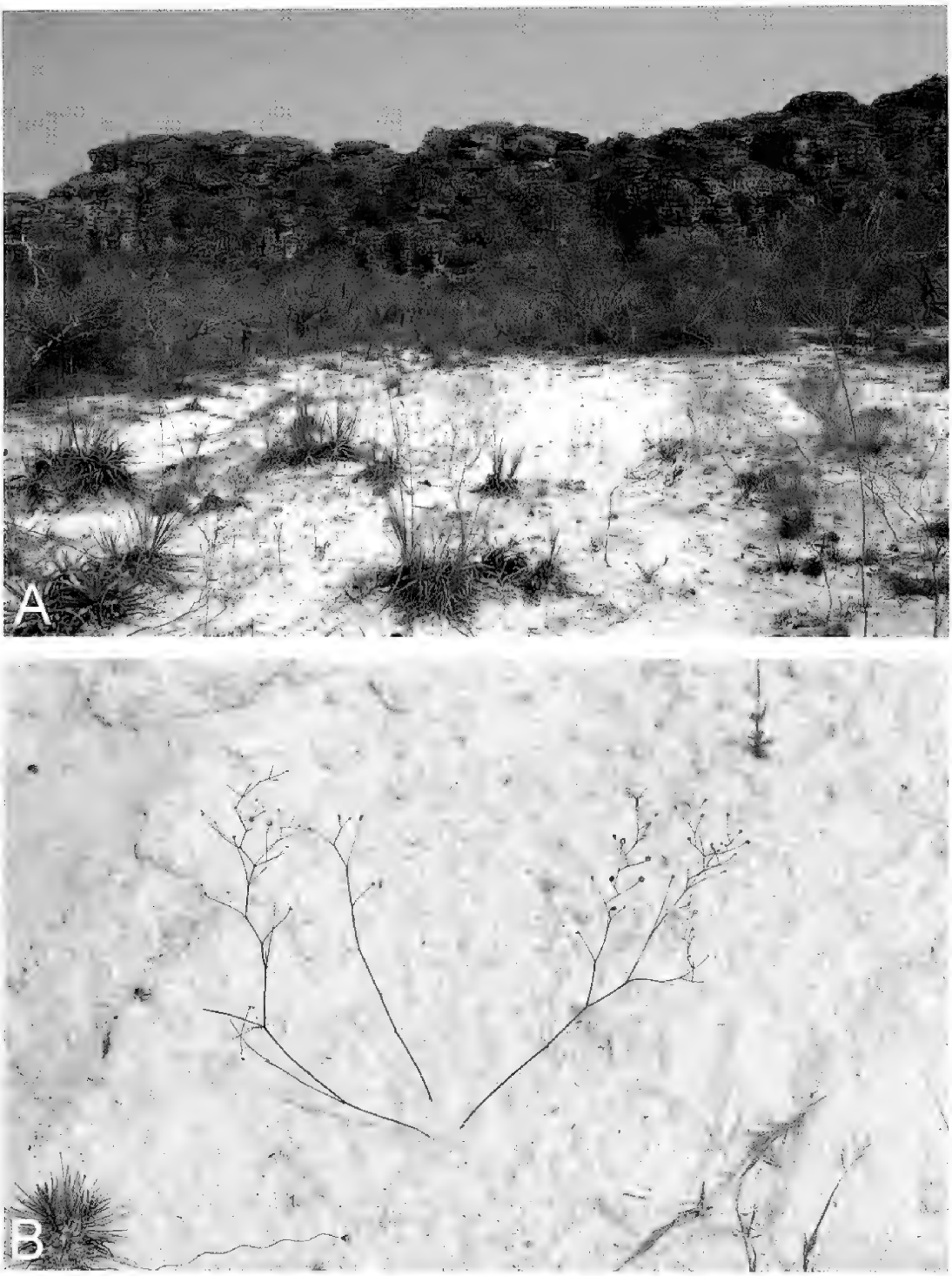


FIGURE 5. Habitat and habit of *Philcoxia minensis* at Serra do Cabral, Minas Gerais, Brazil. A. Habitat. B. Habit in white sand substrate. Photos by F. Almeda.

Hydrotriche (bt = 100; pP = 1.00), *Limnophila* (bt = 95; pP = 1.00), *Gratiola* (bt = 92; pP = 1.00), *Otacanthus* (bt = 72; pP = 1.00), *Stemodia durantifolia* (bt = 82; pP = 1.00), and *Philcoxia* (bt ≤ 50; pP = 1.00). The MP, ML, and BI analyses all recovered identical topologies.

The MP analysis of the expanded core Gratioleae clade with the chloroplast DNA genic regions (24 terminals) recovered seven equally optimal trees of 987 steps (CI = 0.73; RI = 0.76; Fig. 11). In the strict consensus, the species of *Bacopa* form the first-diverging lineage (bt = 100; pP = 1.00). In the sister clade to *Bacopa*, one clade consists of the species of *Scoparia* plus *Leucospora*, *Stemodia suffruticosa*, and *St. verticillata* (bt = 63; pP = 1.00). In the other clade, *Philcoxia* forms the first-diverging lineage (bt ≤ 0.50) whose sister (bt = 80; pP = 1.00) comprises a clade of *Achetaria*, *Otacanthus*, and the other species of *Stemodia* (bt = 75; pP = 1.00), and another of *Amphianthus*, *Dopatrium*, *Gratiola*, *Hydrotriche*, *Limnophila*, and *Sophronanthe* (bt = 80; pP = 1.00). The ML analysis resolved the placement of *Philcoxia* in the same way as did MP, whereas the BI analysis resolved it as sister to the clade of *Leucospora*, *Scoparia*, *St. suffruticosa*, and *St. verticillata* (pP ≤ 0.5). The only difference in the three analyses otherwise is the placement in the BI analysis of *St. durantifolia* as sister to the clade comprising *Achetaria*, *Otacanthus*, *St. glabra*, and *St. schottii* (pP ≤ 0.5) versus as sister to the clade of *Achetaria* and *Otacanthus* (bt ≤ 0.5).

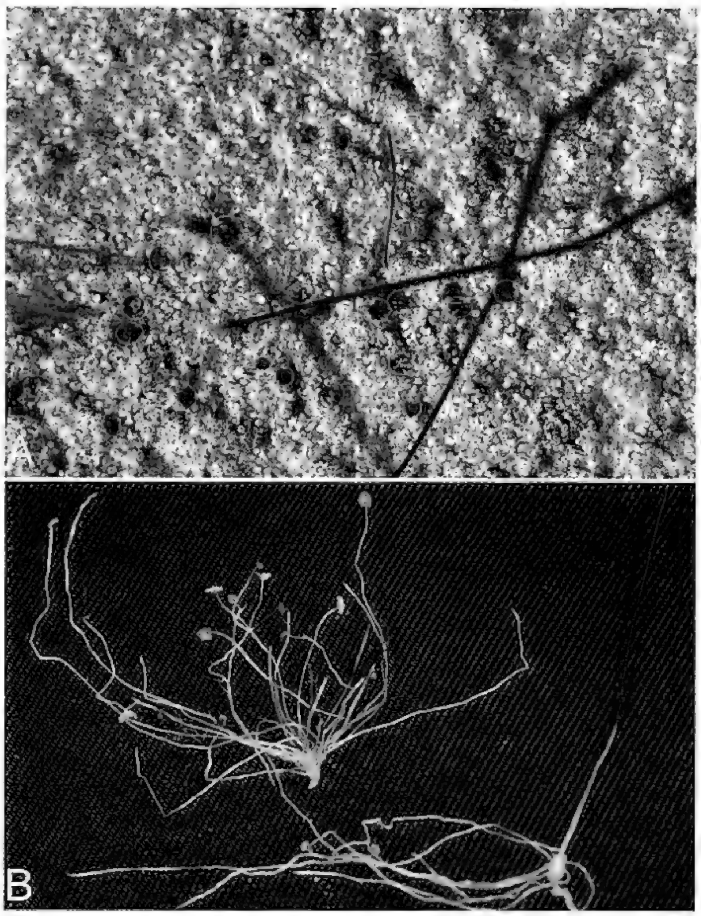


FIGURE 6. Vegetative parts of *Philcoxia minensis* plants. A. Leaf blades on the surface of the white sand substrate. The two intersecting lines in the right half of the image are the basal portions of two peduncles of *Philcoxia*. B. Two upright stems of *P. minensis* with rhizomes, leaves, and (at right) an inflorescence base. Photos by (A) P. Fritsch; (B) F. Almeda.

The ITS and cpDNA data sets were not significantly incongruent as determined from the ILD test ($P = 0.94$). The MP analysis of the combined five-gene expanded core Gratioleae data set (24 terminals) resulted in a single optimal tree of 1394 steps (CI = 0.71; RI = 0.73; Fig. 12). The strict consensus is identical to that recovered from the cpDNA analysis and has higher levels of support. All clades were supported by pP = 1.00. The placement of *Philcoxia* was supported by bt = 52.

TEST FOR CARNIVORY.—The positive control exhibited a strong clear zone where the pineapple touched the film. In all other tests of *Philcoxia* protease activity, no clearing was observed after 12 and 24 hours. After this time some of the plants in the Petri dishes started to die and some clearing occurred but this was likely due to the plants rotting, because the area where the rhizomes/peti-

FIGURE 7. *Philcoxia minensis*, whole plant and inflorescence. A. Single individual removed from substrate. The coin is 2 cm in diam. B. Inflorescences in situ. The flower in the upper right is partly resupinate whereas the two on the lower half of the image are fully so. Photos by (A) F. Almeda; (B) P. Fritsch.

oles contacted the film were also cleared, including that of the negative control. All tests with *Hydrotriche hottoniiflora* and *Limnophila* × *ludoviciana* also returned a negative result.

DISCUSSION

NOTES ON HABITAT AND MORPHOLOGY OF *PHILCOXIA MINENSIS*.—Taylor et al. (2000) stated that species of *Philcoxia* might prefer habitats associated with mining disturbance. The area in

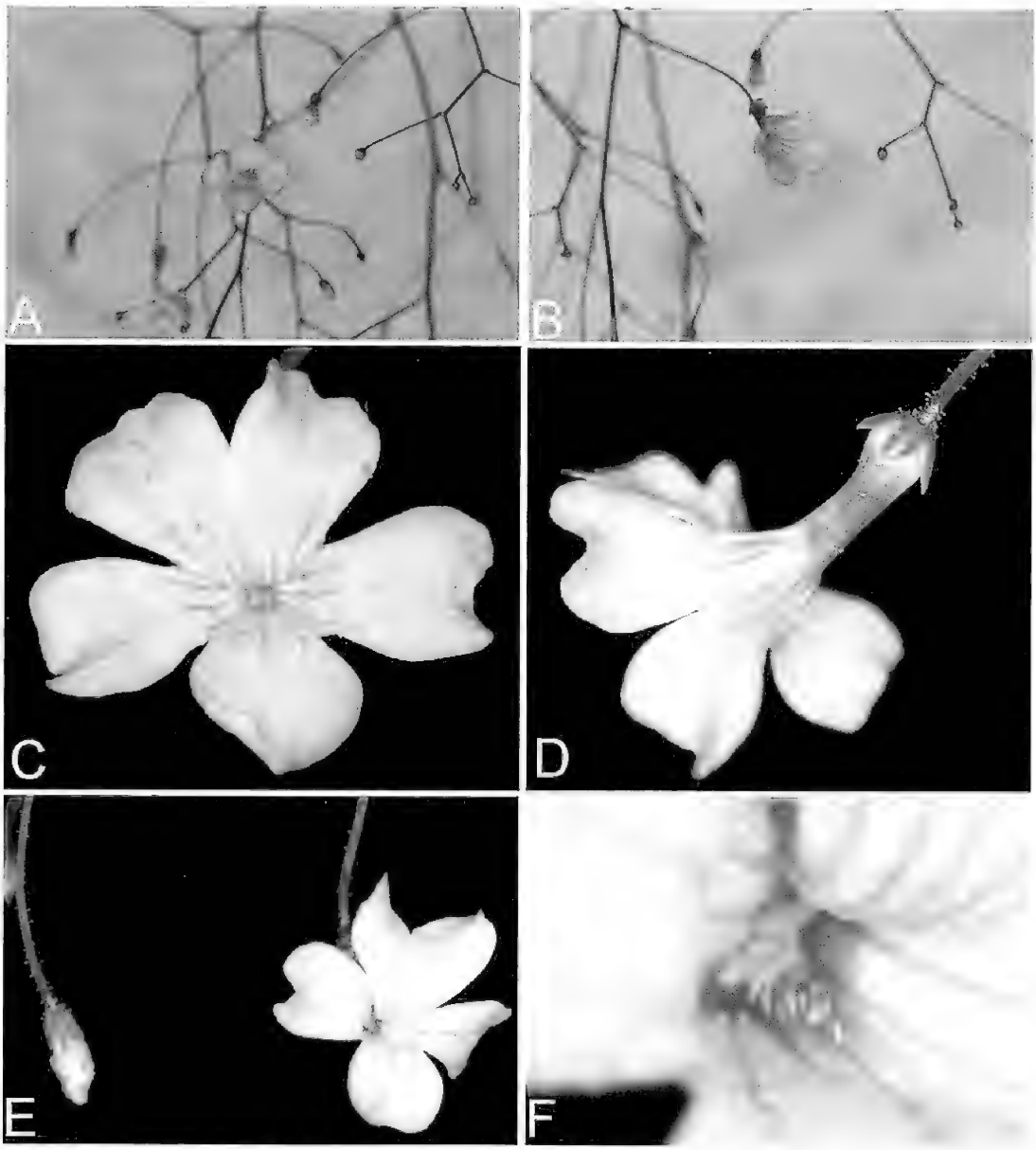


FIGURE 8. Flowers of *Philcoxia minensis*. All flowers are shown with the adaxial half oriented toward the top of the figure. A. Face view. A four-lobed flower. The top edges of the lateral lobes can be seen to be forward of that of the upper lobe, showing that the upper (adaxial) lobe covered the laterals in bud. B. Face-lateral view, showing the adaxial gibbous portion. C. Face view showing three corolla lobes abaxially and two adaxially. D. Upper part of pedicel and flower, rear-lateral view showing adaxial gibbous portion. E. Face-lateral view. F. Close-up of abaxial clavate pubescence. Photos by F. Almeda.

which we rediscovered the species appeared to us to be an undisturbed white sand island surrounded by cerrado. The approximately 50 to100 plants of *P. minensis* we observed occur in a single population across an area of approximately 10 m^2, with several more plants located approximately 30 m distant. Several hours of searching in the surrounding area revealed no additional individuals.

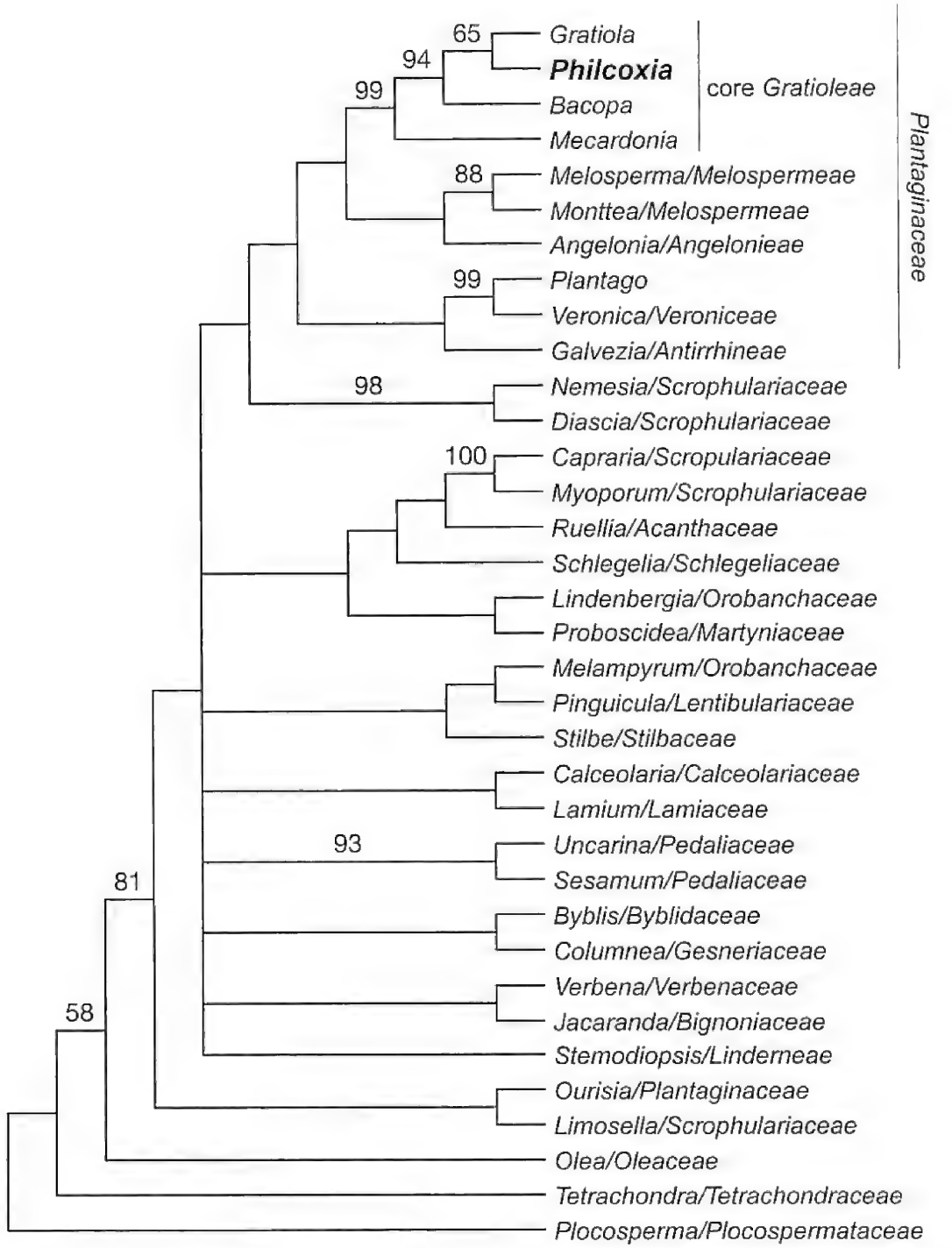


FIGURE 9. Strict consensus of 19 equally shortest trees from a maximum parsimony analysis of Lamiales with 5.8 S nrDNA, *rbcL*, and *trnL-trnF* sequences. Bootstrap values are shown above branches. *Philcoxia* groups strongly within a clade comprising other members of core Gratioleae. Taxon names from Bremer et al. (2002), Fischer (2004), Albach et al. (2005), Oxelman et al. (2005) and R. Olmstead (unpubl. data, available on line at *http://depts.washington.edu/phylo/classifications/Lamiales.html*.).

The species must thus be considered local and rare in the Serra do Cabral region until this area is better known floristically.

Cerrado, the second largest of Brazil's major biomes, is a mosaic of various vegetation types influenced by soil conditions. It is one of the richest of all tropical savanna regions in the world with high levels of endemism (da Fonseca et al. 2004). Estimates indicate that cerrado originally covered from 20 to 25% of the Brazilian territory (Gottsberger and Gottsberger 2006). Despite its geographic extent, cerrado is poorly represented in Brazil's system of protected areas. Current estimates put the size of all protected cerrado areas in Brazil at about 5.5% (da Fonseca et al. 2004). Serra do Cabral currently has no official protected status but it has been identified by the Brazilian government as a priority area of extreme biological importance in the cerrado biome because of its high incidence of endemic plants (Cavalcante and Joly 2002; Costa et al. 1998).

We compared our specimens of *Philcoxia minensis* directly with type material of *P. bahiensis* (*W. Ganev 918*, isotypes: K [96840 and 96841]) and *P. goiasensis* (*H. S. Irwin et al. 14397*, isotypes: K [96839], NY). Taylor et al. (2000) used petiole length, bract length, sepal length, and corolla lobe shape as key characters to distinguish between *P. goiasensis* and *P. bahiensis*/*P. minensis*, and lamina diameter, inflorescence structure, pedicel glandular trichome density, corolla color, and style shape to distinguish between *P. bahiensis* and *P. minensis*. Although most of these character differences are supported by our observations, several are not (Table 3). We consider petiole length in *P. minensis* to vary from 1–30 mm or more, thus overlapping the range of lengths of the other two species. The similarity in the stated corolla color difference (lilac in *P. bahiensis* versus pale

TABLE 3. Morphological character comparison of *Philcoxia bahiensis*, *P. goiasensis*, and *P. minensis* as modified and expanded from the key and descriptions in Taylor et al. (2000).

	P. bahiensis	*P. goiasensis*	*P. minensis*
Root thickness	2–3 mm	ca. 0.2 mm	ca. 1 mm
Rhizome structure	not leaf-bearing	not leaf-bearing	sometimes leaf-bearing
Upright stem structure	branched	unbranched	unbranched
Upright stem thickness	1.5–3.5	0.4–0.6	0.5–1.5
Leaf number per upright stem	numerous (>>20)	6–20	5–10
Petiole length	10–17 mm	2–7 mm	1–30 mm or more
Lamina diameter	1.2–2.5 mm	1.3–2.6 mm	0.5–1.5 mm
Inflorescence structure	simple	simple or branched	simple or branched
Inflorescence length	14–25 cm	9–15 cm	10–26 cm
Inflorescence bract length	0.5–0.8 mm	0.2–0.5 mm	0.5–1.5 mm
Pedicel length	9–16 mm	12–27 mm	10–25 mm
Glandular trichome length on pedicels	to ca. 0.2 mm	to ca. 0.2 mm	to ca. 0.07 mm
Glandular trichome stipe structure on pedicels	uniseriate	uniseriate	simple
Sepal length	1.5–2 mm	ca. 0.7 mm	1–1.5 mm
Corolla tube color[1]	lilac	yellow	pale lavender
Corolla limb width (adaxial to abaxial edges)	8–9 mm	4–5 mm	4–5 mm
Corolla lobe apex shape	emarginate or rounded	all bilobed	undulate, shallowly emarginate, or subtruncate

[1] *P. bahiensis* and *P. goiasensis* only determined from dried material.

lavender in *P. minensis*) renders this character of uncertain utility, although these colors clearly contrast with the yellow tube of *P. goiasensis*. The styles of *P. bahiensis* and *P. minensis*, stated as narrow at the base and widening abruptly towards the apex versus obconic respectively, appear to us to be indistinguishable. Both of them are filiform for the proximal half and flare distally into the stigma.

Irrespective of these and more minor differences in size estimates for various characters, we were able to confirm the distinctness of *P. minensis* as proposed by Taylor et al. (2000). At least five character state differences occur between *P. minensis* and the other two species (Table 3), including the thickness of the root (ca. 1 mm versus ca. 0.2 mm or 2–3 mm), structure of the rhizome (sometimes leaf-bearing versus not leaf-bearing), diameter of the lamina (0.5–1.5 mm versus 1.2–2.6 mm), length of the glandular trichomes on the pedicels (to ca. 0.07 mm versus to ca. 0.2 mm), and the structure of the stipe on the glandular trichomes of the pedicel (simple versus uniseriate).

In contrast to the observations of Taylor et al. (2000) as repeated by Fischer (2004), we did not observe evidence of circinnate vernation either in *Philcoxia minensis* or on the material available to us of the other two species. Instead, the growing tip of the delicate rhizome appears straight or upcurved (Figs. 3C, 6B). Young leaf blades are infolded lengthwise but are not inwardly inclined or coiled. On this basis, circinnate vernation should be removed from any enumeration of features in *Philcoxia* that resemble Lentibulariaceae or other carnivorous plants.

In Gratioleae, the adaxial corolla lobes cover the lateral lobes in bud (antirrhinoid aestivation; Fischer 2004). In *Philcoxia minensis*, the adaxial side is two-lobed or occasionally unlobed, white-pilose internally, and slightly gibbous at the base. The abaxial side has three lobes and clavate puberulence internally, and is the side toward which the stigma is curved. The flowers of *P. minensis* are often resupinate, i.e., with the three-lobed side sky-ward and the two-lobed side ground-ward, through torsion of the pedicel. Sometimes they are positioned at various angles between resupinate and nonresupinate within the same inflorescence (Fig. 7B).

The anther filaments of the two stamens are straight, as in the adaxial stamens of other members of Gratioleae (Fischer 2004). Only a few genera of Gratioleae have pubescent filaments. The filament pubescence in *Philcoxia* appears to be similar to that of *Dopatrium*. Most species of *Dopatrium* have pubescent anthers, in contrast to the glabrous anthers of *Philcoxia*. The knobby thickening just below the anther is here interpreted to be a rudimentary theca. In *Dopatrium* and other members of Gratioleae, the two fertile thecae are disjunct and are attached to the filament by a connective with two arms, each extending to one of the thecae (Fischer 2004). In *Philcoxia*, the flared portion above the sterile theca can therefore be interpreted as an arm of the connective, the other arm of which is absent by reduction if the monothecous condition is derived within the tribe (see below). The transverse orientation of the thecae to the filament in *Philcoxia* is similar to that of species of *Gratiola* excluding *G. hispida* and *G. pilosa*, which belong to *Sophronanthe* (D. Estes, unpublished data).

Although we designate the filamentous structure subtending the lamina as petiolar tissue, this structure and the delicate rhizomes are indistinguishable, at least at 60× magnification. This and the highly variable length of such structures in *P. minensis* lead to the question of whether the structures that are called "petioles" in *Philcoxia* are instead rhizomes, terminated by a sessile leaf blade. In young leaves, the abaxial tissue of the blade appears to be identical to the tissue of the so-called petiole and continuous with it, with the same white color and smooth texture and distinct in color and texture from the young adaxial blade surfaces. The leaves of *Philcoxia* are so unusual that it is possible they are not developmentally or positionally homologous with the leaves of the other members of Gratioleae.

Phylogenetic placement of *Philcoxia*.—Our results strongly support the general place-

ment of *Philcoxia* within tribe Gratioleae, as hypothesized by Taylor et al. (2000) and Fischer (2004). Other members of Gratioleae *sensu* Fischer (2004: at the subfamily level) have a combination of the following characters: glandular trichomes pluricellular-headed; inflorescences racemose; corollas often two-lipped, unspurred; adaxial corolla lip not galeate, covering the lateral lobes in bud; stamens two to four (rarely five in *Bacopa*), the abaxial pair often reduced to staminodes or lacking; anther thecae rounded at base; and ovary bilocular. The morphology of *Philcoxia* agrees well with these characters, with its two-lipped, unspurred corolla; non-galeate adaxial corolla lip that covers the lateral lobes in bud; two stamens, the abaxial pair lacking; rounded anther thecae; and bilocular ovary. The inflorescence of *Philcoxia* is unique in the tribe in its single bract per node (versus two per node) and zig-zag pattern of branching. This has made the basic structure of the inflorescence (racemose versus cymose) difficult to interpret from morphology alone. The unequivocal placement of *Philcoxia* in the Gratioleae demonstrated here supports the interpretation of the inflorescence as racemose as in other members of the tribe, rather than cymose as suggested by Souza (1996).

The results do not support the specific hypothesis put forward by Taylor et al. (2000) and Fischer (2004) of a close relationship of *Philcoxia* to *Dopatrium*, *Hydrotriche*, or *Limnophila*. In our analyses, these three genera form a clade that is sister to *Amphianthus*, *Gratiola*, and *Sophronanthe*, whereas *Philcoxia* is placed as sister to this clade plus *Achetaria*, *Otacanthus*, and *Stemodia* in part. This specific placement of *Philcoxia* received BI support of 1.00 but bt support of only 52 in the combined analysis, probably resulting from the very long branch of *Philcoxia* in both ITS and the cpDNA results (Figs. 10–12), thus leaving the specific placement of *Philcoxia* somewhat in question.

The characters defining the informally named subtribe "Dopatriinae" by Fischer (2004; i.e., the three genera above plus *Deinostema*) are plants mostly aquatic; bracteoles absent (except some species of *Limnophila*); flowers with two stamens, the abaxial pair usually reduced to staminodes or lacking; anthers with two separate thecae held together by a connective with two short arms; and seeds reticulate (smooth in some *Limnophila*). From our observations can be added the presence of chambered stems, and opposite or verticillate bracts and leaves. Of these characters, *Philcoxia* agrees only in the lack of bracteoles and presence of two stamens with abaxial staminodes lacking. Otherwise, it is terrestrial, the stems are solid, the bracts and leaves (and rhizome branches) are alternate, the anthers are monothecous, and the seeds are foveolate-reticulate. *Philcoxia* is the only genus in the tribe *sensu* Fisher (2004) with monothecous anthers.

Even with the limited sampling conducted here of the core members of tribe Gratioleae, results indicate that *Philcoxia* forms a distinct lineage relative to other members and this accords well with the unusual morphological features of the genus. The available data are unable to place *Philcoxia* with high confidence, but results are resolved enough to clearly establish that *Philcoxia* groups somewhere above *Bacopa* and *Mecardonia* as opposed to highly nested within the tribe. Although additional sampling may affect the interpretation of character state evolution in *Philcoxia*, the available data establish that the subterranean stems and petioles, peltate leaves, zigzag inflorescence, solitary inflorescence bracts, and monothecous anthers all represent uniquely derived character states within core Gratioleae. The addition of other genic regions and other taxa will be required to determine the precise placement of *Philcoxia* and provide more comprehensive statements of character state evolution. For now it is clear that because of the relatively basal placement of *Philcoxia* demonstrated here, it will be critical to include this genus in any tribe-wide assessments of character state evolution.

NEGATIVE EVIDENCE OF CARNIVORY.—Givnish (1989) has listed two requirements for a plant to be classified as carnivorous: it must be able to absorb nutrients from dead animals next to its sur-

faces, and it must have some morphological, physiological, or behavioral feature whose primary effect is the active attraction, capture, and/or digestion of prey. Thus, the inducement of proteases on the surface of leaves would go far toward demonstrating carnivory in particular plant species and the protease test employed here has been used to help distinguish between carnivorous plants, or those likely to be so (*Dionaea*, *Drosera*, *Drosophyllum*, *Pinguicula*, *Stylidium*), versus noncarnivorous plants (*Byblis*, *Ibicella*, *Proboscidea*, *Roridula*; Hartmeyer 1997; Meyers-Rice 1999; Darnowski et al. 2006), especially *in lieu* of detailed nutrient uptake experiments. The negative results for protease activity obtained for *Philcoxia* suggest that it is not carnivorous.

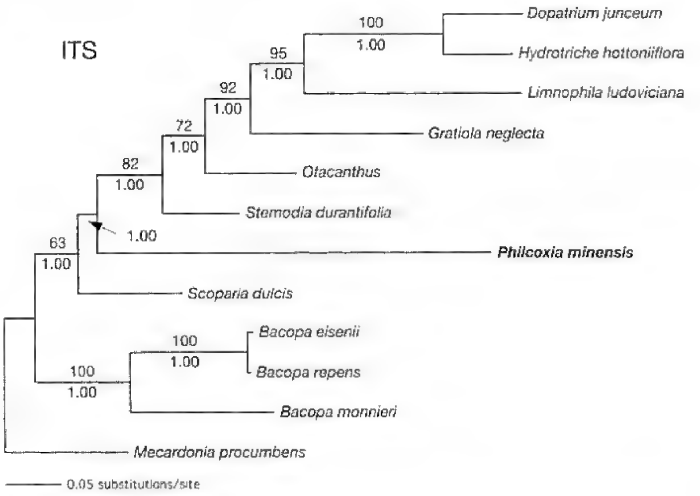
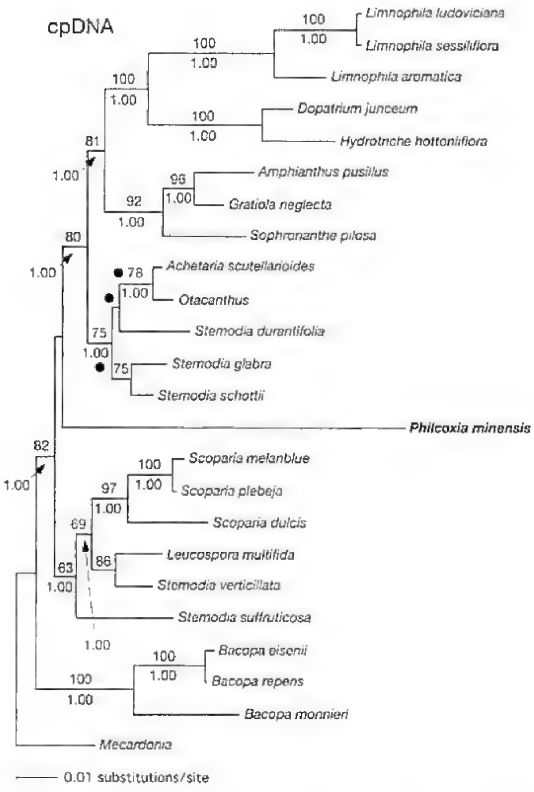


FIGURE 10. The single best maximum likelihood tree (= the single maximum parsimony and 50% majority-rule Bayesian inference trees) from analysis of core Gratioleae with ITS sequences. Bootstrap values >50% are shown above branches; posterior probabilities >50% are shown below branches.

There are several potential sources of error, however, that might have affected our ability to detect a positive test result for carnivory in *Philcoxia minensis*. First, the small leaf blades of *P. minensis* (0.5–1.5 mm diam.) on delicate petioles were difficult to manipulate, and the hemispherical shape of the blades with glands on the convex side restricted the area of leaf surface in contact with the surface of the film; flattening the blade to obtain more contact risked crushing the leaf tissue. A more reliable test would likely come from using one of the other two species of *Philcoxia*, because their leaves are substantially larger than those of *P. minensis*. *Philcoxia bahiensis* might be best suited for the test because it appears to have the most glands per unit area of leaf of any of the three species. Further, a known population is extant in Bahia, whereas *P. goiasensis* has not been rediscovered (Taylor et al. 2000). Second, the test might not have been sensitive enough to detect protease activity. Our trial tests with a species of *Pinguicula* failed to produce clearing on the film, whereas species of *Drosera* produced a dramatic area of clearing. In the case of *P. minensis*, the leaves are so small that they might not have been able to digest enough of the film for any clearing to be observed. Third, it is possible that *P. minensis* is carnivorous for only part of the year or under certain environmental conditions. Several of the known carnivorous plants show seasonality in carnivory (e.g., *Sarracenia*, *Stylidium*; Givnish 1989; Darnowski et al. 2006). A major environmental factor that the habitat of *Philcoxia* does not seem to share with that of known carnivorous plants is high water availability. When we sampled *Philcoxia* (late September and October), no water was detected in the white sand substrate, but this probably changes during the rainy season. If *Philcoxia* is actively digesting soil organisms only at times of adequate soil moisture, it would be critical to sample protease activity during these times. This becomes more likely when one considers that because many soil nematodes are drought-tolerant through anhydrobiosis (Demeure et al. 1979), carnivory could be timed to the rainy season when nematodes are active.

It would be desirable to be able to grow plants of *Philcoxia* under controlled conditions to be



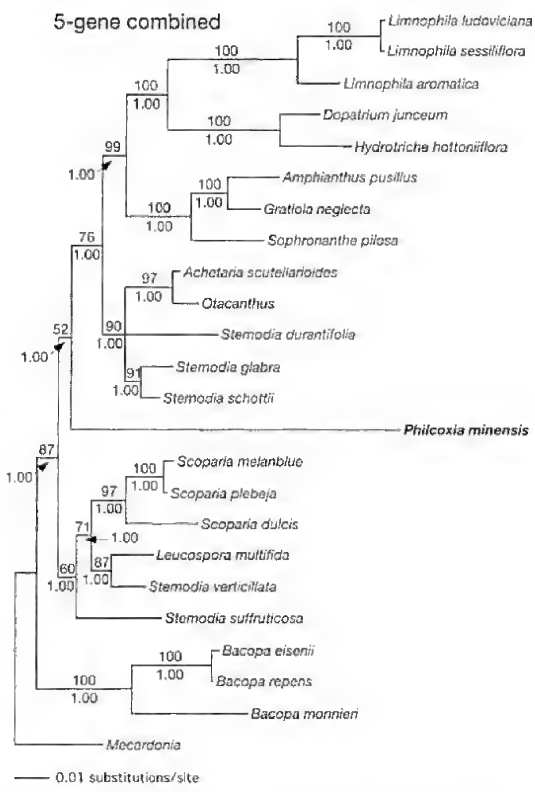


FIGURE 11 (left). The single best maximum likelihood (ML) tree from analysis of core Gratioleae with cpDNA sequences (*trnL-trnF*, *rbcL*, *matK/3′-trnk*, and *3′-ndhF*). Dots indicate clades that collapse in the strict consensus of seven equally optimal trees in the maximum parsimony (MP) analysis; other clades in the MP analysis are identical to those recovered from ML. The tree from Bayesian inference is identical to that from the ML analysis except that the placement of *Philcoxia* is as sister to the clade comprising *Leucospora*, *Scoparia*, *Stemodia suffruticosa*, and *St. verticillata* ($pP \leq 0.5$) and the placement of *St. durantifolia* is as sister to the clade comprising *Achetaria*, *Otacanthus*, *St. glabra*, and *St. schottii* ($pP \leq 0.5$). Bootstrap values >50% are shown above branches; posterior probabilities >50% are shown below branches.

FIGURE 12 (right). The single best maximum likelihood (ML) tree (= the single maximum parsimony and 50% majority-rule Bayesian inference trees) from analysis of core Gratioleae with combined ITS, *rbcL*, *trnL-trnF*, *matK/3′-trnk*, and *3′-ndhF* sequences. Bootstrap values >50% are shown above branches; posterior probabilities >50% are shown below branches.

able to conduct additional tests for carnivory, but our attempts to maintain the plants collected in the field or to grow them from seed have been unsuccessful. Until then, on the basis of our tests we assume that *Philcoxia* is not carnivorous and an alternative explanation must be sought for the unusual growth form, leaf shape, and abundance of glands on its leaf surfaces. One possible explanation for the habit of the species is that the plants could merely be adapted to the hot and dry environment in which they occur in keeping most of their parts underground, with only the mature leaf surfaces and inflorescences above the surface of the soil. The glandular hairs could thus serve as a defense against herbivory by small animals crawling on the surface of the soil. The glands also could provide a physical protective function against sharp sand grains, which could otherwise cut and injure the leaves. More study of *Philcoxia* in this context is clearly needed to understand the evolution of this highly unusual plant.

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PROCEEDINGS OF THE CALIFORNIA ACADEMY OF SCIENCES

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A New Genus and Species of Mud-Dwelling Moray Eel (Anguilliformes: Muraenidae) from Indonesia

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Diaphenchelys pelonates **genus and species novum, subfamily Muraeninae, is described from three specimens collected along mud slopes at 15–32 m off Maumere Bay, Flores Island, Indonesia.** ***Diaphenchelys*** **differs from all known muraenids in collectively having an elongate body, a short snout, moderately elongate jaws that are not strongly recurved, biserial maxillary dentition with an inner row of enlarged conical teeth, and mean vertebral formula 6/56/154. Although most similar in appearance to species of** ***Gymnothorax*****, it is most closely related to species of** ***Enchelycore*****. The occupation of mud habitats is very uncommon for muraenids and the facial coloration and pore reduction adaptations of the new species are probably linked to that habitat.**

During three diving expeditions to Flores, Indonesia, the second author observed a species of moray eel living along a mud slope in Maumere Bay. Unable to recognize it, he collected and photographed three individuals, shared them with the senior author, and after careful examination we were unable to assign them to any known muraenid genus. At first appearance, they appear similar to species of *Gymnothorax* (*sensu lato*), however, upon closer examination of the teeth and other characteristics, we were unable to place them within any known subgenus of *Gymnothorax*. They share several specializations with the species of *Enchelycore* but lack the prominent hooked jaws, elongate neurocranium, and other specializations of those species. Mud bottoms are not common habitats for most morays and we suspect that some of the distinctive characters of the new species are associated with living in mud. Pending a comprehensive revision of the family Muraenidae, we are cautious in describing a new genus along with our new species; however, we remain satisfied that in the evolution of moray eels, this too is a monotypic muraenid endeavor.

Materials and Methods

Measurements are straight-line, made either with a 300 mm ruler with 0.5 mm gradations (for total length, trunk length, and tail length), and recorded to the nearest 0.5 mm, or a 1 m ruler with 1 mm gradations and recorded to the nearest 1 mm. All other measurements are made with dial calipers or dividers and recorded to the nearest 0.1 mm. Proportions are expressed in terms of total length (TL), measured from the snout tip to the end of the tail, or head length (HL). Body length is head plus trunk length. Head length is measured from the snout tip to the posterodorsal margin of the gill opening; trunk length is taken from the end of the head to mid-anus; body depth is measured at the gill opening and at the anus and does not include the fins; body width is measured imme-

diately behind the gill openings and above the anus; snout length is measured from the snout tip to the anterior margin of the eye; upper-jaw length is measured from the snout tip to the external inner angle of the mouth; lower-jaw length is measured from the tip of the lower jaw to the external inner angle of the mouth. Head pore terminology follows that of Böhlke et al. (1989). Vertebral counts (which include the hypural) are obtained from radiographs as described by Böhlke (1982); the mean vertebral formula (MVF) is expressed as the mean value for predorsal/preanal/total counts. Tooth counts are approximate and include sockets of missing teeth. Institutional abbreviations follow Leviton et al. (1985). Osteological examination was based on radiographs, dissection, and cleared and stained specimens, prepared using the method of Dingerkus and Uhler (1977).

Diaphenchelys McCosker and Randall, gen. nov.

TYPE SPECIES: *Diaphenchelys pelonates* McCosker and Randall, sp. nov.

ETYMOLOGY.— From the Greek *diaphoros*, different, and *enchelys*, eel, treated as feminine according to Opinion 915 of the Bulletin of Zoological Nomenclature, 1970. The generic name refers to the anatomical characteristics and the unusual habitat preference of the type species.

DIAGNOSIS.— Body elongate, laterally compressed throughout trunk and tail; head and trunk shorter than tail. Dorsal-fin origin closer to gill opening than to gape. Snout short, rear margin of orbit above middle of jaw; jaws moderately elongate, not strongly arched, nearly closing completely. Anterior nostril tubular, anteriorly-directed; posterior nostril an elongate slit above and anterior to eye, its margin smooth. Gill opening below midside, small and slitlike. Head pores reduced in number and size; 2 branchial pores. Teeth conical, sharp and prominent, some enlarged, but no large fangs; maxillary teeth biserial, the inner row larger, the outer numerous and closely spaced; mandibular teeth mostly uniserial, a few inner large teeth and outer row numerous and closely spaced. Neurocranium not elongate; gill arches typically muraenine, hypobranchials 1-2 absent; 7 branchiostegal rays. Coloration of body and tail brown with pale markings on head and throat.

RECOGNIZED SPECIES.— A monotypic genus.

REMARKS.— The combination of characters identified in the diagnosis (particularly the short snout and the dentition) separates this monotypic genus from all known morays. Comparisons to species of other muraenine genera are included in the remarks following the description of the new species.

No modern comprehensive study of the Muraenidae has been attempted and published. The only complete osteological study of a moray was that of *Muraena helena* by Böhlke et al. (1989). Nelson (1966) presented a comparative analysis of muraenid gill arches and identified subfamilial differences between the species of the 12 genera that he examined. Gill arches of the new species are similar to those of *Gymnothorax rueppelliae* (Nelson 1966: figs. 42–44, as *G. petelli*) and *Muraena helena* (Bohlke et al. 1989: fig. 113). Fielitz (2002) reported on pectoral bones (presumably representing the scapula and coracoid) within the Muraenidae and found their condition to be variable (and inconsistent) within and among the subfamilies. The condition of the pectoral bones of *Diaphenchelys pelonates* is similar to that of several muraenine species and identical in appearance to his illustration (Fielitz 2002: fig. 2) of the pectoral array of *Gymnothorax griseus*. At this time neither he nor we accord that condition any phylogenetic significance.

The hyoid skeleton and branchial basket of morays are reduced. Hyoid reduction has been related to the moray behavior of lunging and biting their prey rather than suction-feeding (Mehta and Wainwright 2007). Böhlke et al. (1989:111) commented on branchial reduction in morays and observed in *Muraena helena* that the non-overlapping slender branchiostegal rays are closely followed by the slender cleithrum and supracleithrum, which function, if at all, like additional bran-

chiostegal rays. This appears similar to the condition of the new species, whose further reduction may be attributable to its mud-inhabiting lifestyle. The possession of only seven pairs of branchiostegal rays by *Diaphenchelys pelonates* sets it apart from most muraenines. Our survey is far from comprehensive; however, our sampling of species from several other muraenine genera found all except *Echidna nebulosa* to possess eight or more pairs. We found the following: *E. nebulosa* seven; *Enchelycore schismatorhynchus*, *Gymnothorax castaneus* and *Rhinomuraena quaesita* eight; *Muraena helena* eight or nine; and *Enchelycore bayeri*, *E. nigricans*, *Gymnomuraena zebra*, and *Gymnothorax reticularis* nine. We also analyzed (by clearing and staining, radiography and dissection) five species (*Anarchias cantonensis*, *Scuticaria tigrina*, *Uropterygius macularius*, *U. marmoratus* and *U. polyspilus*) of uropterygiines. None of them appeared to possess any branchiostegal rays. Christopher Fielitz (*in litt.*), however, advised us that three minute branchiostegal rays may be present on a 128 mm cleared-and-stained specimen of *Anarchias similis* that he examined. We are hesitant to infer any phylogenetic significance to this character until a more extensive evaluation is made.

***Diaphenchelys pelonates* McCosker and Randall, sp. nov.** Mud-dwelling moray
Figures 1–7.

Material Examined.— Holotype: BPBM 32205, 465 mm TL, male, Indonesia, Flores, Maumere Bay, off Sao Wisata Resort (08°37′49.15″S, 122°18′45.75″E), collected in 30–32 m along a mud slope by J.E. Randall, R.H. Kuiter, and L.C. Reynolds, 19 Sept. 1987. Paratypes: CAS 214523 (formerly BPBM 36688), 364 mm TL, female with developing ova (~0.6–0.8 mm), cleared and stained, from same location as holotype, collected in 19.5 m along a mud-and-isolated-rock slope by J.E. Randall, 9 Nov. 1990. BPBM 34128, 121 mm TL (tail damaged, foreshortened, and healed), sexually immature, from same location as holotype, collected in 15–17 m along a sloping mud bottom with burrows of varying size by J.E. Randall, 18 Sept. 1988.

Diagnosis.— A small, elongate, slender brown moray with white spots and vermiculations on head behind rictus and extending into anterior trunk; fins with pale margins posteriorly; anus before midbody, preanal length 2.5–2.6 in TL; depth at gill opening 33-35 in TL; head 10–11 in TL; snout short, rear margin of orbit above middle of eye; jaws moderately long, not notably recurved; teeth conical, some needle-like; maxillary teeth biserial, those of outer row smaller and closely spaced; mandibular teeth mostly uniserial, the outer row smaller and closely spaced; MVF 6/56/154.

Measurements (in mm) and counts of the holotype.— Total length 465; head length 43.7; preanal length 179; snout to dorsal-fin origin 30.3; depth at gill opening ~16.5; depth at anus ~15; width at gill opening ~11.5; width at anus ~10.5; length upper jaw 16.3; length lower jaw 15.8; snout length 5.5; eye diameter 3.0; fleshy interorbital width 4.2. Predorsal vertebrae 6, preanal vertebrae 58, total vertebrae 155.

Description.— An elongate (Figs. 1–2), slender moray, depth at gill opening 33–35, depth at anus 32–36 in TL; anus before midbody, preanal length 2.5–2.6 in TL. Head moderate, 10–11 in TL; snout short, 7.9–8.8 in HL; jaws moderately elongate, upper jaw 2.6–3.1 in HL (jaw proportionately longer in larger specimens); jaws of 2 smaller specimens close completely, those of holotype slightly recurved; eye moderate in size, its diameter 12.2–14.5 in HL, closer to snout tip than to rictus, its rear margin above middle of jaw. Minute papillae within mouth. Anterior nostril in a short, anteriorly-directed tube, reaching halfway to tip of snout or jaw margin; posterior nostril an elongate slit above and anterior to eye, its margin smooth. Dorsal-fin origin above first branchial pore, closer to gill opening than to rictus. Skin above origin of dorsal fin flabby, loose. Gill opening a small slit below midside. Predorsal vertebrae 4–6, preanal vertebrae 55–58, total vertebrae 153–155 (excludes smaller paratype which has 147 total vertebrae; its tail appears damaged and foreshortened); MVF 6/56/154.

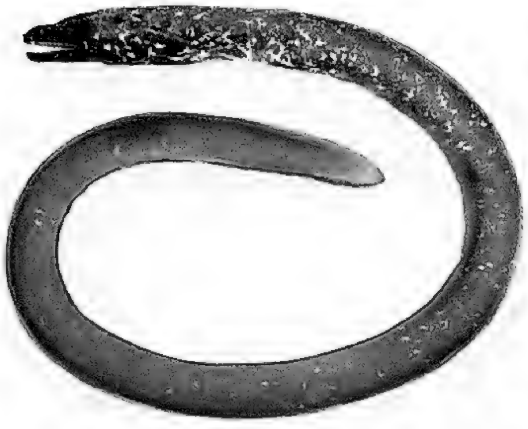

FIGURE 1. Holotype of *Diaphenchelys pelonates* sp. nov., BPBM 32205, male, 465 mm TL. Photographed by J.E. Randall soon after its capture.

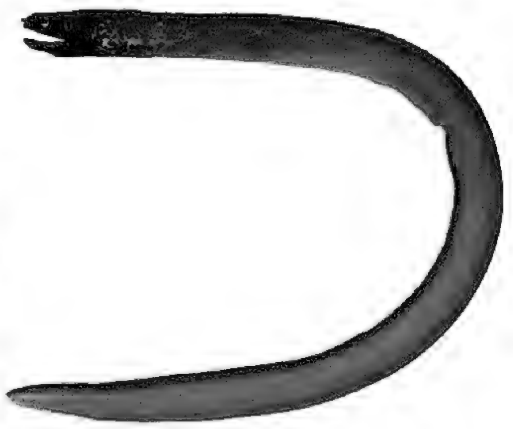

FIGURE 2. Paratype of *Diaphenchelys pelonates* sp. nov., BPBM 34128, sexually immature, 121 mm TL (the tail is damaged, foreshortened, and has healed). Photographed by J.E. Randall soon after its capture.

Head pores (Fig. 3) typical but reduced in number, most (except mandibular, supraorbital, and anterior infraorbital) reduced in size and barely discernible; supraorbital 1+2; infraorbital 4 (holotype and larger paratype have 4 IO pores, smaller paratype has additional pore beneath posterior margin of eye); mandibular 6 left, 7 right; 2 minute branchial pores above and anterior to gill opening.

Gill arches (Figs. 4–5) typical of muraenine condition (Nelson 1966); similar to those of *Gymnothorax petelli* (=*G. rueppelliae*) (Nelson 1966: figs. 42–44) and *Muraena helena* (Böhlke et al. 1989: fig. 113). Hypobranchials absent; third infrapharyngobranchial ossified; upper tooth plate a fusion of third and fourth plates, with same-sized, pointed, recurved teeth; three tooth pairs followed by nine uniserial teeth; lower pharyngeal tooth plate lies on medial surface of proximal end of fourth ceratobranchial, which fits into groove within plate, with pointed, recurved teeth of same size as those of lower plate, with three pairs followed by 13 uniserial teeth. No teeth of plates enlarged. Upper plate is 94% length of lower plate. Seven threadlike branchiostegal rays originate ventrad to epihyal, preopercle and interopercle, oriented anterodorsally toward lateral-line canal.

TABLE 1. Counts and proportions (in thousandths) of the holotype and paratypes of *Diaphenchelys pelonates*. TL = total length. HL = head length. Dorsal-fin origin is measured from radiographs. Counts and measurements involving the total length of the smallest paratype are excluded because its tail is damaged and foreshortened.

	Holotype	*Mean*	*Range*
TL (mm)	465	—	121-465
HL/TL	94	97	94-100
Head and trunk/TL	385	394	385-404
Tail/TL	615	606	596-615
Depth at gill opening/TL	35	34	33-35
Dorsal-fin origin/TL	65	68	65-71
Upper jaw/HL	373	367	363-373
Snout/HL	126	130	113-150
Eye/HL	69	77	69-82
Predorsal vertebrae	6	6	6
Preanal vertebrae	58	56	55-58
Total vertebrae	155	154	153-155

Teeth (Fig. 6) conical, recurved; no large fangs, however 3 ethmoidal teeth near tip of mandible enlarged. Upper jaw contains a pair of small intermaxillary teeth straddling midline of snout, followed by 6 uniserial conical teeth on each side, those followed by an outer row of 30 small, closely-spaced nearly triangular teeth and an inner row of 7–8 larger conical teeth. About 5–6 short, small teeth hidden within skin folds flanking vomer. Lower jaw teeth mostly uniserial, a pair, followed by 4 larger conical pairs, then an outer row of 25–26 closely-spaced small teeth (similar in shape

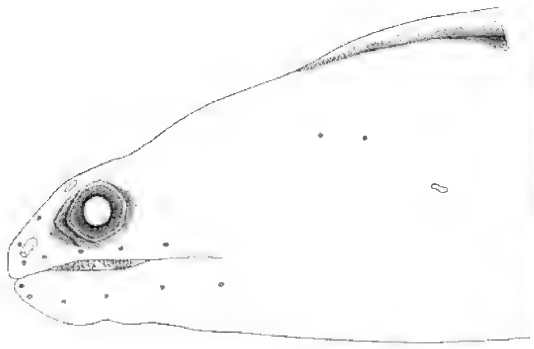

FIGURE 3. Head of holotype of *Diaphenchelys pelonates* sp. nov., BPBM 32205, male, 465 mm TL. Drawn by S. Hernandez.

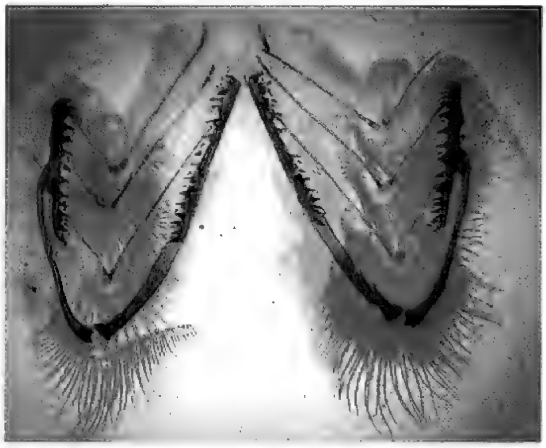

FIGURE 4. Gill arches (interior view, cut longitudinally along ventral surface and spread laterally) of paratype of *Diaphenchelys pelonates* sp. nov., CAS 214523, 364 mm TL, a female. Bone is stained red and cartilage is blue.

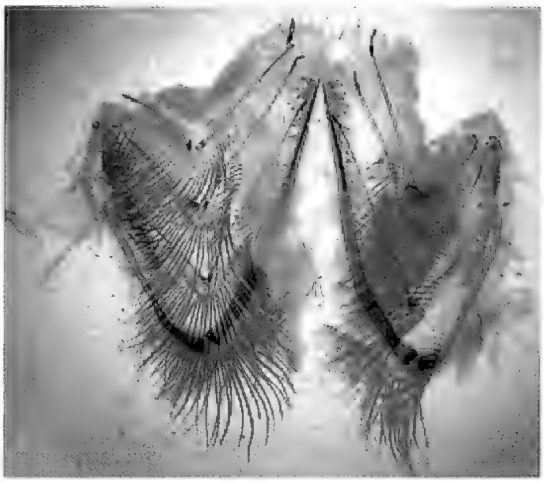

FIGURE 5. Gill arches (exterior view, cut longitudinally along ventral surface and spread laterally) of paratype of *Diaphenchelys pelonates* sp. nov., CAS 214523, 364 mm TL, a female. Bone is stained red and cartilage is blue.

and size to outer row of maxillary teeth), descending in size, reaching rictus.

Body coloration in ethyl alcohol (Figs. 1–2) tan to brown, overlain on trunk and head with irregular mosaic of white spots and markings (less so on juvenile), primarily in throat region, extending about a head's length posteriorly. Anterior region of head forward of rictus darker brown and lacks pale mottling. Snout, chin, gular area, anterior nostrils, tongue and palate dark brown. Inner lip margins and gums pale. Gill openings and cephalic pores pigmented like surrounding tissue. Anterior ⅔ of dorsal fin brown like body, its margin becoming pale in posterior half of tail. Anal fin dark brown at base, its margin pale, notably contrasting with body. Peritoneum pale.

SIZE.— The largest known specimen is a 465 mm TL male.

ETYMOLOGY.— Named *pelonates*, from the Greek *pelos*, mud, and *nates*, dweller, treated as a noun in apposition.

DISTRIBUTION.— Known only from Maumere Bay, Flores, Indonesia, living over a mud-and-rock bottom, between 15 and 32 m depth.

REMARKS.— It is unlikely that the new species would be mistaken for any other known Indo-Pacific moray eel. The new species differs from all known morays in its combination of diagnostic characters, including its slender, elongate body, its dentition, its short snout and anteriorly located eye, its brown coloration with pale head and trunk markings, its reduced cephalic pores, and in its vertebral formula.

Diaphenchelys pelonates is a small species, the 364 mm female paratype being sexually mature. The habitat in which all known specimens have been observed, soft-mud slopes, might explain its dark snout and chin, as well as the reduction and minute nature of some of its pores (particularly the supraorbital and infraorbital cephalic pores) as a means to avoid clogging. Similar pore

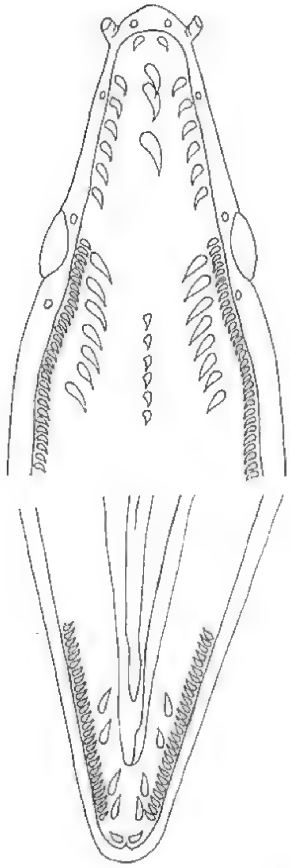

FIGURE 6. Semidiagrammatic illustration of dentition of holotype of *Diaphenchelys pelonates* sp. nov., BPBM 32205, male, 465 mm TL. Drawn by S. Hernandez.

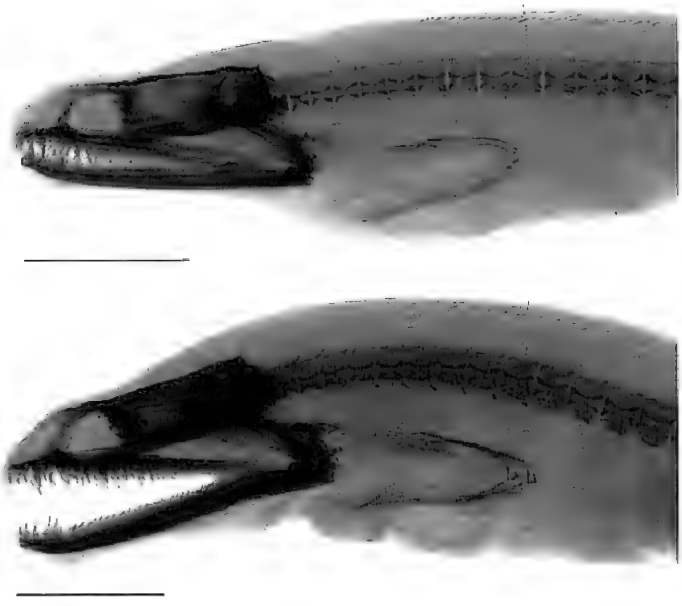

FIGURE 7. Radiographs of neurocrania of *Diaphenchelys pelonates* sp. nov. Top: paratype, CAS 214523, 364 mm TL. Bottom: holotype, BPBM 32205, male, 465 mm TL. Scale indicates 1 cm.

reduction and head coloration can be seen in certain ophichthids that occupy sand and mud burrows (McCosker et al. 1989; McCosker and Randall 2001), often with only their eyes, snout and jaws exposed.

As stated above, the new species first appeared to belong to *Gymnothorax*, differing primarily in the anterior position of its eye; the rear margin of the orbit of species of *Gymnothorax* is located behind mid-jaw. The dentition and jaws of the new species suggest that its affinities lie closer to *Enchelycore*. (We recognize that *Gymnothorax* and *Enchelycore*, as currently recognized, are probably polyphyletic.) Similarities lie in the elongate inner row of mandibular teeth and the tendency toward jaw elongation and curvature with growth (as evidenced by the holotype). The species of *Enchelycore* are elongate, with their tail typically longer than their body, and notably, most possess slender, elongate, strongly arched jaws that are incapable of closing completely (Böhlke et al. 1989). As well, their neurocrania are elongate and depressed, unlike that of *Diaphenchelys* which is neither depressed nor elongate (Fig. 7). Other characters of *Enchelycore* include the short, tubular, anterior nostrils (except those of *E. schismatorhynchus*, which are enlarged), posterior nostrils oval and typically above or before the eye (except those of *E. pardalis* which are within elongate tubes), and jaw teeth that are conical, sharp, and partly biserial (those of the outer row much smaller than those of the inner row). Species vary in size from small (*E. carychroa* to about 335 mm, and *E. nycturanus*, known only from three immature 206–223 mm specimens) to quite large (*E. schismatorhynchus* to 1200 mm). Some species (such as *E. nigricans* and the *D. pelonates*) have contrasting patterns of blocks, blotches, and streaks, becoming uniformly dark as adults; others (such as *E. pardalis*, *E. nycturanus* and *E. anatina*) are strikingly patterned with pale blotches and spots, and dark spots, that pattern becoming more exaggerated in adults. And finally, species such

as *E. bayeri*, *E. bikiniensis*, *E. carychroa*, and *E. octaviana* are nearly uniform in their coloration from juvenile through adults. (*Enchelycore ramosus* is known only from a few adult specimens; the coloration of young fish is not known.) The only *Enchelycore* known to approximate its vertebral formula are *Enchelycore anatina* (*D. p.* 6/56/154, *E. a.* 7/56/154), a widely-distributed trans-Atlantic species captured from depths of 10–380 m (Böhlke et al. 1989: 136–140), and *E. nycturanus* (6/55/147), an Indian Ocean species known only from Kwazulu-Natal, South Africa (Smith 2002).

Diaphenchelys pelonates thus appears more closely related to the twelve known species of *Enchelycore*, rather than to species of *Gymnothorax*, in possessing comparable dentition and general body proportions, as well as the similarity in coloration differences between juveniles and adults of some species. Only the holotype of *D. pelonates*, however, has any indication of possessing recurved jaws. Examination of the ontogeny of jaw elongation of *Diaphenchelys pelonates* as seen in radiographs (Fig. 7) and by measurement of the snout/jaw relationship (Table 2) suggest that the new species approaches this condition but falls far short of that of species of *Enchelycore*.

TABLE 2. Proportion of snout length to upper jaw length in *Diaphenchelys* and *Enchelycore*. Data sources: 1) this study; 2) Böhlke et al. (1989); 3) Böhlke and Smith (2002); 4) Böhlke and Böhlke (1976); 5) Randall and McCosker (1975); 6) Smith (2002).

Species	*Snout/upper jaw*	*Source*
D. pelonates	.333	1
E. anatina	.500	2
E. bayeri	.511	3
E. bikiniensis	.434	3
E. carychroa	.418	4
E. kamara	.400	3
E. lichenosa	.417	3
E. nigricans	.391	2
E. nycturanus	.487	6
E. octaviana	.535	3
E. pardalis	.533	3
E. ramosus	.468	5
E. schismatorhynchus	.500	1

COMPARATIVE MATERIAL EXAMINED.— Specimens examined either by radiography and dissection (X) or by clearing and staining (CS); all measurements represent total length. **Subfamily Uropterygiinae**: *Anarchias cantonensis* CAS 57411, 145 mm (CS). *Scuticaria tigrina* CAS 90440, 755 mm (X). *Uropterygius macularius* CAS 29123, 202 mm (CS). *U. marmoratus* CAS 55335, 570 mm (X). *U. polyspilus* CAS 108959, 445 mm (X). **Subfamily Muraeninae**: *Echidna nebulosa* CAS 37340, 263 mm (X). *Enchelycore bayeri* CAS 28675, 320 mm (CS); CAS 28692, 266 mm (X); CAS 37243, 117-259 mm (X); CAS 28675, 310 mm (X). *E. bikiniensis* CAS 99270, 255 mm (X); CAS 63228, 160 mm (X). *E. carychroa* CAS 13490, 135-282 (X). *E. lichenosa* (holotype of *Aemasia lichenosa*) CAS-SU 6480, 527 mm (X). *Enchelycore nigricans* CAS 31695, 243 mm (CS); CAS 31695, 200-510 (X). *E. octaviana* SU 52651, 298 mm (X). *E. pardalis* CAS 214522, 197 mm (X). *E. schismatorhynchus* CAS 28726, 285 mm (CS); CAS 28676, 266 mm (X); CAS 28677, 271 mm (X); CAS 65770, 365 (X). *Gymnomuraena zebra* CAS 37262, 165 mm (CS); CAS 53706, 261 mm (X). *Gymnothorax castaneus* CAS 27513, 238 mm (CS). *G. funebris* CAS 154204, 342 mm (X). *G. griseus* CAS 63219, 210 mm (X). *G. reticularis* CAS 33933, 260 mm (CS). *G. tile* CAS 50934, 187 mm (X). *Muraena helena* ANSP 128117, 460 mm (CS and skeletonized). *Pseudechidna brummeri* CAS 99372, 685 mm (X). *Rhinomuraena quaesita* CAS 55912, 1010 mm (CS); CAS 24293 950 mm (X).

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